

ANNALE

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J A A R G A N G 35 R E E K S A N O. 1—4 (1959)

ONTOGENY OF THE BREAST-SHOULDER APPARATUS OF THE SOUTH AFRICAN LACERTILIAN, *MICROSAURA PUMILA PUMILA* (DAUDIN)

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'N STUDIE VAN DIE LIGGAAMSBOU EN LIGGAAMSGROEI VAN BLANKE EN KLEURLINGSEUNS IN DIE WESTELIKE PROVINSIE, OUDERDOMSGROEP 13 TOT 17 JAAR

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A STUDY OF MALE SOMATOTYPES AMONG THE SOUTH AFRICAN BANTU MINE LABOURERS COMPARED WITH OTHER GROUPS (SHELDON'S NOMENCLATURE)

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ON THE CLOACAL REGION OF ANURA in Particular of Larval *Ascaphus*

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by

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(With 28 text-figures)

Thesis accepted for the Degree of Doctor of Science
at the University of Stellenbosch

Promotor: Professor C. G. S. de Villiers

Submitted: November 1958

ABSTRACT

The ontogeny of the breast-shoulder apparatus has been investigated. The sternum arises as two discrete, longitudinal anlagen which, for a short time, appear to be continuous with the cartilagine coracoideae. Fusion of these anlagen occurs only after they have been joined by three pairs of sternal ribs. The sternum in the adult animal is an "unsegmented", fenestrated cartilage with an ossified perichondrium. The so-called "xiphi-sternum" is of non-costal origin and is derived from the same anlagen as the sternum proper. The formative intersternal tissue is actively skeletogenous and contributes towards the formation of the "praesternum". The coracoid is an unfenestrated, partially ossified structure arising from a single anlage, and possesses a foramen for the n. supracoracoideus. Membrane bones are lacking in the adult breast-shoulder apparatus, but a clavicle and interclavicle appear for a short time during ontogeny. The clavicle is eventually replaced by the sterno-coracoid ligament. In the adult the m. deltoideus inferior (m.d. claviculæ) consists of two separate bellies, but they have a single anlage with origo on the clavicular vestige in the embryo.

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PART I

I INTRODUCTION

This investigation was undertaken at the suggestion of Prof. C. G. S. de Villiers, who was the first of the Zürich school to break away from the classical costal theory of Ruge (1880). Ruge derived the sternum from the ventral ends of the ribs. De Villiers (1922) demonstrated that the sternum of *Bombina* and *Alytes* is partly of zonal and partly of inscriptional origin.

The sternogenesis of *Amphibia* and *Mammalia*, especially that of man, has received considerable attention from embryologists and comparative anatomists, but that of *Reptilia* and *Aves* has been somewhat neglected. The morphology of the sternum of the different classes of the *Vertebrata* is still a much disputed problem in comparative anatomy; the final answer to this question can only be given after extensive research has been carried out in the sternogenesis of a great number of vertebrates. Comparatively little has been done on the ontogeny of the shoulder-girdle itself. It is a well-known fact that the zonal and appendicular skeleton develop from the same anlage; the origin of the mother tissue of this anlage, however, is unknown, since no known stains will differentiate tissue derived from the axial mesenchyme from that of the cutis layer of the myotome. The anlage of the shoulder-girdle is generally believed to be of sclerotomic origin (De Villiers, 1926).

The shoulder-girdle and the sternum have received considerable attention from W. K. Parker (1868) who introduced the names "praesternum", "meso-sternum" and "xiphisternum" for the various parts of the lacertilian sternum. These names are still used although they are purely topographical and have no morphological significance. The term "breast-shoulder apparatus" was introduced by Fürbringer (1900) to denote the shoulder-girdle and the sternum conjointly. The investigations of Parker (1868) and Fürbringer (1873, 1874, 1876 and 1900) were confined to adult anatomy and contained no embryological details.

The breast-shoulder apparatus of *Lacerta* (Fig. 1) consists of a rhomboidal, fenestrated sternal plate, a flat, fenestrated coracoid, a scapula, a cartilago suprascapularis and two membrane bones: the clavicle and the interclavicle. The antero-lateral edges of the sternum are grooved for the reception of the coracoids, while the first three pairs of sternal ribs articulate with the postero-lateral sternal edges. The ventral ends of the fifth pair of sternal ribs articulate with the posterior end of the sternal plate and are joined by those of the fourth pair to form the so-called "xiphisternum".

Parker (1868) called the inferior cartilaginous margin of the lacertilian coracoid the "epi-coracoid" and a portion of its anterior cartilaginous expansion the "prae-coracoid". Götze (1877) found these terms unacceptable, since the coracoid of *Cnemidophorus* develops from a single, unfenestrated anlage. His work was later confirmed for other genera by Bogoljubski (1914), van Gelderen (1924-25) and Fuchs (1927). The lacertilian coracoidal fenestrae are therefore secondary features ("Reduktionsfenster" of Fuchs) resulting from a reduction of the original coracoidal anlage. The unchondrified tissue gives rise to the membranes ("Reduktionsmembranen" of Fuchs (1927)) covering these fenestrae. Such fenestrae are not homologous with the fenestra situated in the ventral part of the anuran shoulder-girdle. This latter is bounded by the

coracoid, cartilago procoracoidea and the pr. epicoracoideus and is to be regarded as a primary fenestra ("Sprossungsfenster" of Fuchs).

The breast-shoulder apparatus of the *Chamaeleontidae* differs markedly from that of the typical *Lacertilia*: the coracoid is unfenestrated and resembles that of the *Rhynchocephalia*; moreover, the apparatus entirely lacks membrane bones.

Götte (1877) and Wiedersheim (1892) were the first to contribute to the sternogenesis of the *Lacertilia* and came to the same general conclusion: they derived the sternal anlagen from the ventral ends of the ribs and thus

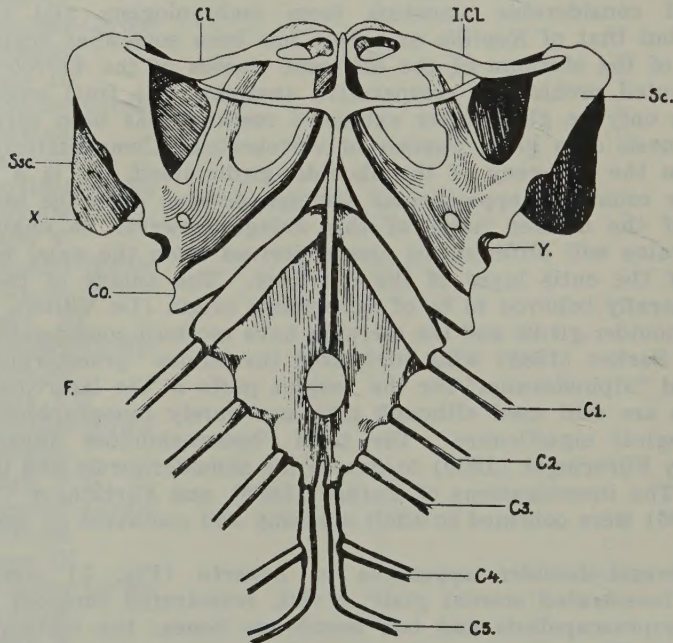


Figure 1.

Breast-shoulder apparatus of *Lacerta muralis* (after Juhn, 1923). C1—C5, thoracic ribs; Cl., clavicle; Co., coracoid; F., fenestra sterni; I.Cl., interclavicle; Sc., scapula; Ssc., suprascapulare; x., foramen for the n. supracoracoideus; y., fossa glenoidalis.

confirmed Ruge's costal theory for *Lacerta* and *Cnemidophorus*. Recent contributions to the sternogenesis of the *Lacertilia* are those of Bogoljubski (1914), Van Gelderen (1922a and 1924-25) and Juhn (1923). Both Van Gelderen and Bogoljubski derive the "praesternum" of *Lacerta* from autochthonous anlagen. Juhn, however, maintains that the sternum is a derivative of the ventral ends of the ribs. When the sternal anlagen appear the ventral ends of the sternal ribs are in continuity with them, thus, according to Miss Juhn, confirming Ruge's costal theory.

In the first part of this paper a number of embryonic stages, covering the ontogeny of the sternum and the shoulder-girdle, are described. The second part is a summary and discussion of the morphological problems involved.

II MATERIAL AND TECHNIQUE

The material used in this investigation was collected at Stellenbosch where the Cape Dwarf Chamaeleon is quite common. The name *Microsaura* was based by Gray (1864) upon the features of the species *M. melanocephala*; he proposed the generic name *Lophosaura* for *Chamaeleo pumilus* described by Daudin in 1802 (vide Fitzsimons, 1943). The name *Lophosaura* was generally accepted until Fitzsimons (1943) pointed out that it had already been given by Gray in 1852 to a South American lizard. Fitzsimons proposed the generic name of *Microsaura*, originally given to the species *melanocephala* by Gray (1864), for the small South African viviparous chamaeleons which are referred to as the *pumilus* section of the genus *Chamaeleon* by Methuen and Hewitt (1913), the other members of the genus being oviparous.

About 30 developmental stages, ranging from 10 mm. to 27 mm. were collected. The embryos were measured from the tip of the snout to the cloacal (actually the urodeal) aperture. Since the number of embryos obtained from each female varied from 8 to 20, enough material was available for transverse, sagittal and frontal sections. It was therefore unnecessary to use any base-line for orientation. Ten stages were selected for detailed description and graphic reconstruction. In addition to these, three juveniles and one young adult male were microtomed. Serial sections were cut at 8 μ , 10 μ , 15 μ and 20 μ , depending upon the age of the specimen.

In this Institute vertebrate embryological material is generally fixed in corrosive sublimate, Allen's or Bouin's fluid, the first giving uniformly better results with avian material. Corrosive sublimate was also tried out for the chamaeleon embryos but Bouin's fluid gave infinitely better results. Specimens were kept in 70% alcohol after fixation; they may be kept in the fixative for a prolonged period without danger of overfixation. The picric and acetic acid in the Bouin make decalcification of the younger embryos unnecessary. Some workers recommend the use of a few drops of a saturated solution of lithium carbonate to remove the picric acid, but it was found not to be detrimental and easily washes out in the 70% alcohol in which the specimens are kept after fixation. Bouin's fluid proved to be an excellent fixative giving uniformly good results with a variety of differential stains.

The older embryos were decalcified in a 6% solution of concentrated nitric acid in 70% alcohol, and in Ebner's fluid, the latter being preferable for older specimens. A juvenile specimen was decalcified by means of prolonged immersion in Müller's fluid, an excellent decalcifying agent, its only disadvantage being that it works very slowly. The use of nitric acid cannot be recommended for decalcification of freshly fixed juvenile and adult material, since the alcohol hardens the connective tissue and ligaments, thus impairing the infiltration of the paraffin. This method, however, gave excellent results in the case of embryological material.

Xylol was used as a clearing agent, and the embryos were imbedded in paraffin with a melting point of 52°C. Hard paraffin was not employed

in the case of the juvenile and adult specimens, since much better results were obtained with a softer paraffin (m.p. 46-48°C).

Various methods of staining were employed. Reptilian procartilage and embryonic cartilage do not stain satisfactorily with azan; Bismarck-brown and eosin were therefore employed as plasmal stains with Heidenhain's iron-hematoxylin. Eosin was occasionally omitted. This method proved very useful for demonstrating the first signs of deposition of the intercellular matrix. Staining with Mayer's acid-hemalum was also tried, but the results were unsatisfactory. Older embryos, juveniles and adult specimens were stained in toto with borax-carmin and counterstained with azan. This method was very useful for demonstrating the first signs of perichondral ossification and of membrane bones; the osseous tissue stains brightly with the aniline blue.

Section drawings were made with the aid of a micro-projector and were used in making graphic reconstructions according to Pusey's (1939) method. The study of the muscles was greatly facilitated by the use of a wax-plate model of the breast-shoulder apparatus of a juvenile specimen. In addition a large specimen was cleared in KOH. The bones and cartilage were stained in alizarine red and toluidine blue according to the Lundvall (1927) method.

III ACKNOWLEDGEMENTS

It was under the supervision of prof. C. G. S. de Villiers that this work was carried out. I wish to express to him my sincere thanks for his constant advice and assistance.

I also wish to thank dr. M. E. Malan for having read the manuscript.

I am extremely grateful to the Council for Industrial and Scientific Research for the award of a Research Scholarship.

IV DESCRIPTION OF DEVELOPMENTAL STAGES

A STAGE I

Length of embryo: 13.5 mm.

Shoulder-Girdle

The anlage of the shoulder-girdle is present as a mass of actively condensing blastematos tissue lacking a definite outline, so that it is not possible at this stage to draw a sharp line of demarcation between the anlage itself and the surrounding tissue. For this reason a graphical reconstruction of the shoulder-girdle cannot be very accurate. However, the elements of the girdle and the limb skeleton can be readily identified as a dorsal pars scapularis, a distal pars humeralis projecting into the limb bud and a ventral pars coracoidea enclosing the n. supracoracoideus. Proximally, near the locality of the fossa glenoidalis, the cells of the anlagen of the pars scapularis and of the pars humeralis are rounder in outline and faint traces of intercellular deposit, staining faintly with Bismarck-brown, can already be detected.

Sternum

In this stage the future anlagen of the sternum cannot yet be identified. The site of those of its anlagen which are expected to arise medio-ventral to the apices of the myotomes, is occupied by loose blastematous tissue, which is continuous medially with the blasteme derived from the axial mesenchyme and laterally with similar tissue derived from the cutis layer of the myotome. There is no histological difference between cells of sclerotomic and those of dermatomic origin, so that it is impossible to say whether cells occupying the site of the future anlagen of the sternum, are exclusively sclerotomic or of dermatomic origin, or of both.

B STAGE II

Length of embryo: 13.9 mm.

Shoulder-Girdle

The shoulder-girdle anlage has undergone notable changes: cell differentiation has commenced, and the different parts of the shoulder-girdle can now be readily identified although the humerus is still in blastematous continuity with the girdle. The anlagen of the muscles of the shoulder-girdle and the humerus now appear for the first time (Fig. 2). The pars scapularis is procartilaginous in the region of the glenoid cavity and projects dorsally as a strand of dense blastematous tissue into the body-wall up to a point antero-lateral to the blastematous tip of the first cervical rib. The pars coracoidea is a planar patch of dense tissue in which faint traces of intercellular substance can be seen in the part adjoining the pars scapularis. Ventral to the glenoid cavity the foramen for the n. supracoracoideus is situated. Although the humerus is still in blastematous continuity with the shoulder-girdle its caput and pr. medialis are easily distinguishable as dense tissue containing faint traces of intercellular deposit. In the shaft of the humerus chondrification has already commenced.

Cell differentiation has also started in the myocommata, with the result that the anlagen of the two cervical ribs and the first thoracic rib consist of procartilage or of dense mesenchyme.

Sternum

The earliest discrete anlagen of the sternum are present as two strands of thick blastematous tissue in the lateral body-wall behind the postero-ventral end of the planum coracoideum (Fig. 3). It lies medio-ventral to the anlagen of the intercostal and zonal musculature. Its anterior tip lies immediately posterior to the planum coracoideum and is continued medio-ventrally to the anlagen of the intercostal musculature, up to a point immediately behind the blastematous tip of the third thoracic rib (Fig. 4). The anlage originates as a condensation of the mesenchyme medio-ventral to the intercostal and zonal musculature and is separated from the planum coracoideum by a layer of loose connective tissue.

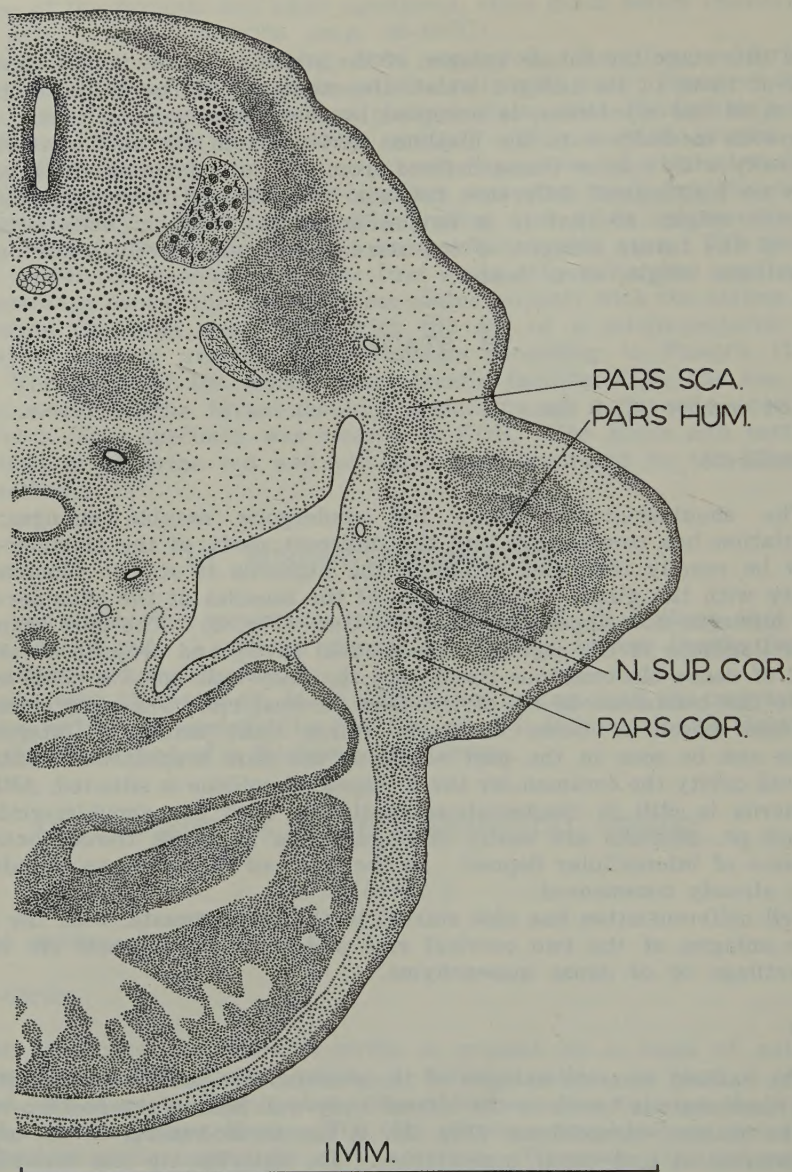


Figure 2.

Transverse section through the anlage of the shoulder-girdle of a 13.9 mm. embryo. N. SUP. COR., nervus supracoracoideus; PARS COR., pars coracoidea; PARS HUM., pars humeralis; PARS SCA., pars scapularis.

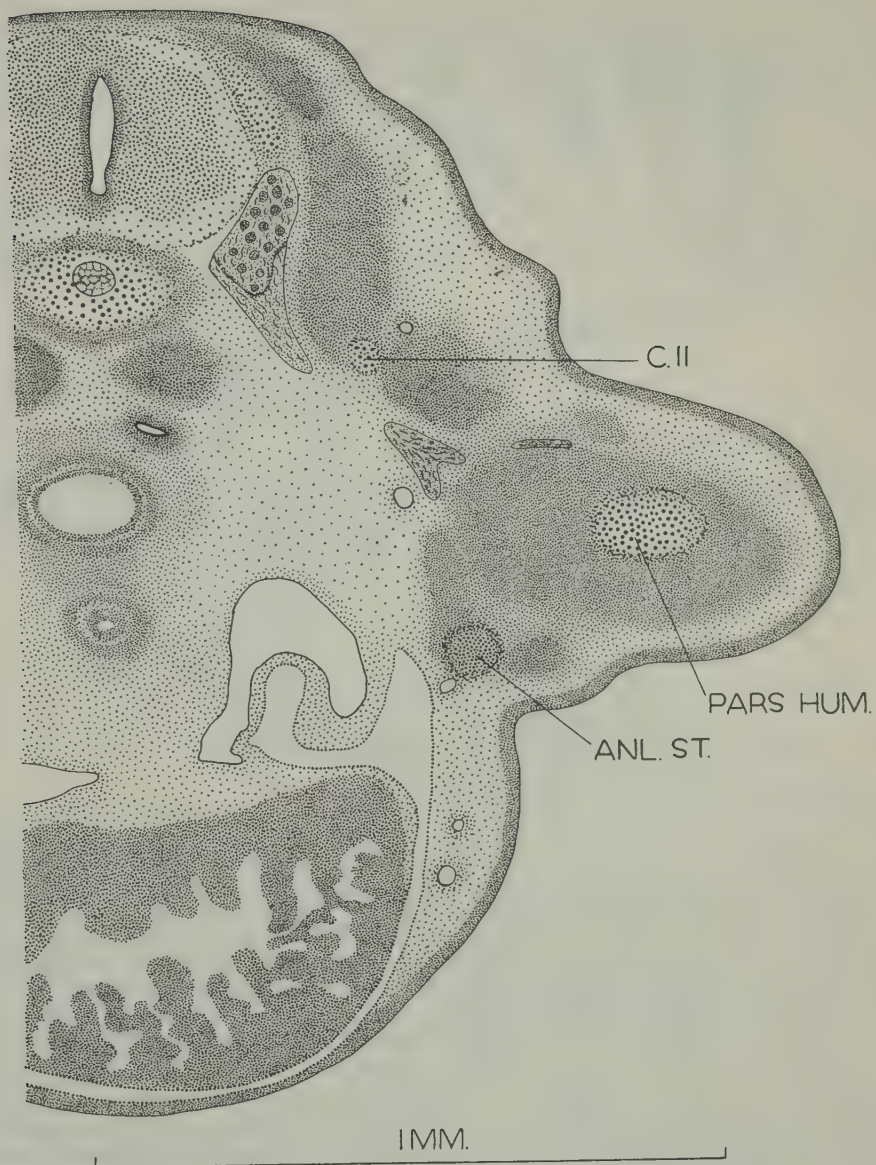


Figure 3.

Transverse section through the sternal anlage of a 13.9 mm. embryo.
 ANL. ST., anlage of the sternum; C. II, second cervical rib; PARS HUM.,
 pars humeralis.

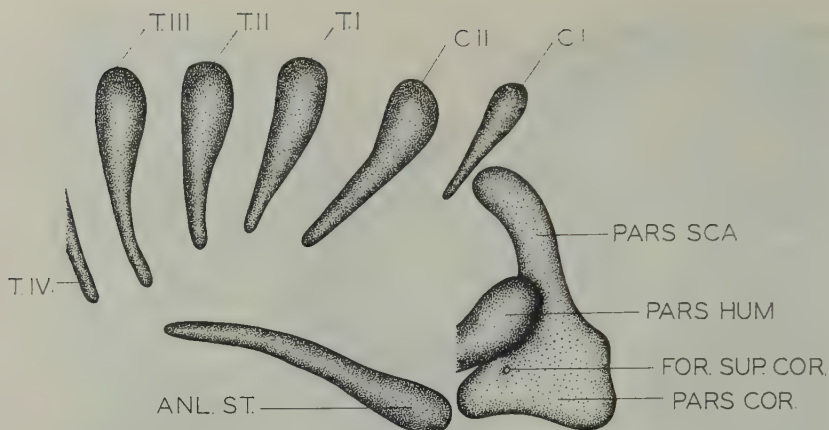


Figure 4.

Graphic reconstruction of the breast-shoulder apparatus of a 13.9 mm. embryo. X66.6. Norma lateralis. ANL. ST., anlage of the sternum; C.I and C.II, cervical ribs; FOR. SUP. COR., foramen for the n. supratoracoides; PARS COR., pars coracoidea; PARS HUM., pars humeralis; PARS SCA., pars scapularis; T.I—T.IV, thoracic ribs.

C STAGE III

Length of embryo: 16.2 mm.

Shoulder-Girdle

Chondrification has now commenced, and the cartilago scapulo-coracoidea has assumed its adult form, although the two halves of the shoulder-girdle are still widely separated ventrally. Considerable change is noted in the pars scapularis: the cartilago scapularis has lengthened dorsally and has extended postero-dorsally as the pars suprascapularis. Its shaft has chondrified, while the broad dorsal pars suprascapularis which now covers the first cervical rib, is still procartilaginous. Ventrally the cartilago scapularis has also changed considerably: the postero-ventral end has thickened to form the upper part of the fossa glenoidalis while anteriorly a protuberance has developed on the border between the cartilago scapularis and the cartilago coracoidea. Fürbringer (1900) calls it the "prominentia coraco-scapularis" since in the adult condition a clavícula is absent and the protuberance consists partly of the coracoid and partly of the scapula and is therefore not homologous with the acromion of the other *Lacertilia*. Ventrally the planum coracoideum has increased in size. Chondrification has commenced in the part adjoining the pars scapularis in the region of the fossa glenoidalis. Starting from this single centre of chondrification, the planum coracoideum gradually becomes procartilaginous up to its anterior, ventral and posterior borders; but this

structure remains fringed with persistent, dense connective tissue. The shaft of the humerus is entirely chondrified, and although the caput humeri is still in syndesmotic continuity with the cartilago scapulo-coracoidea, the glenoid cavity, the caput humeri, the pr. medialis and the pr. lateralis can already be distinguished. The distal part of the humerus has not been studied.

Sternum

Anteriorly the two halves of the sternum have now expanded in a medio-ventral direction so that their anterior tips lie medio-ventral to the ventral border of the planum coracoideum (Fig. 5). In transverse sections

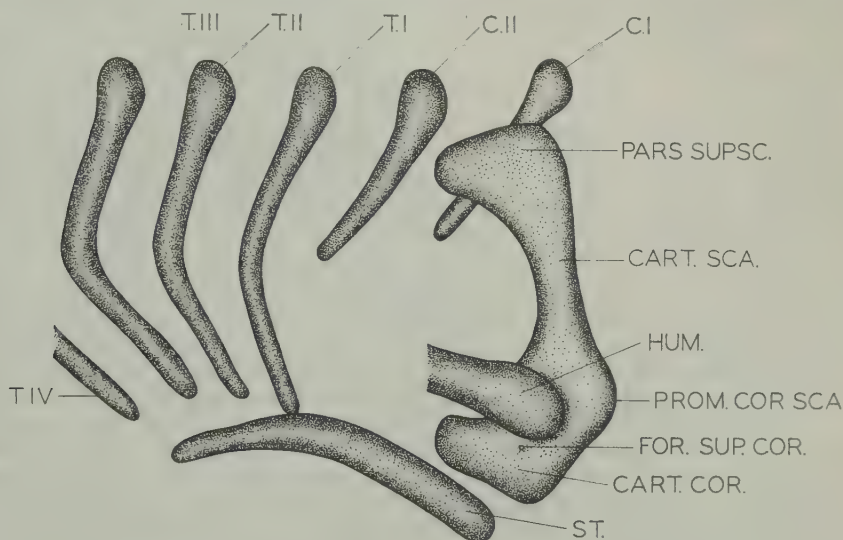


Figure 5.

Graphic reconstruction of the breast-shoulder apparatus of a 16.2 mm. embryo. X66.6. Norma lateralis. C.I and C.II, cervical ribs; CART. COR., cartilago coracoidea; CART. SCA., cartilago scapularis; FOR. SUP. COR., foramen for the n. supracoideus; HUM., humerus; PARS SUPSC., pars suprascapularis; PROM. COR. SCA., prominentia coraco-scapularis; ST., sternum; T.I—T.IV, thoracic ribs.

the anterior portions of the two halves of the sternum appear as areas of dense blastematos tissue medio-ventral to the cartilago coracoidea; they are separated from the latter by means of loose embryonic connective tissue. Posterior to the cartilago coracoidea they appear in section as procartilaginous structures lying medial to the anlagen of the partes sternales musculorum pectoralium and ventral to the anlagen of the intercostal musculature. Chondrification has also started in the cervical and first thoracic ribs. Ventrally the first pair of thoracic ribs is already connected with the sternum;

the junctional regions consist of blastematos tissue in which traces of intercellular deposit can already be detected. The ventral ends of the second and third pairs of thoracic ribs still consist of dense blastematos tissue and are still entirely discrete from the sternum. Behind the connexion of the first pair of sternal ribs with the sternum, the latter is still in a dense blastematos condition, but traces of intercellular deposit are already evident. Each half of the sternum continues as a strand of dense blastematos tissue up to a point immediately posterior to the blastematos tip of the third thoracic rib.

D STAGE IV

Length of embryo: 18.5 mm.

Shoulder-Girdle

The two halves of the girdle now occupy a more ventral position. The shaft of the cartilago scapularis has elongated so that the pars suprascapularis now covers the middle part of the first cervical rib and the dorsal part of the second. The ventral part adjoining the cartilago coracoidea has narrowed as a result of reduction of the posterior tuberosity dorsal to the glenoid fossa. Further chondrification of the planum coracoideum has taken place and it has extended in a postero-ventral direction. In the proximal portion of the humerus—which has chondrified completely—the general contours of the mature bone can already be seen. The fossa glenoidalis is well developed, but there is as yet no synovial cavity, the area between the caput humeri and the fossa glenoidalis being occupied by dense embryonic connective tissue.

This stage is characterized by the appearance of the clavícula, which appears in section as a diminutive patch of bony tissue staining blue with azan; it appears in only two consecutive $10\ \mu$ sections (Fig. 6), and is embedded in embryonic connective tissue situated ventro-medial to the anlage of the m. deltoideus clavicularis (m. d. coraco-sternalis s. inferior of Fürbringer) and ventral to the anterior end of the cartilago coracoidea. In an intermediate stage (17.8 mm.) the anlage of the clavícula appears ventral to the cartilago coracoidea and consists of a discrete patch of thickened embryonic connective tissue. It is impossible to ascertain the origin of the cells in this patch of tissue since the area in which it occurs is in direct histogenetic continuity with embryonic tissue derived from the cutis layer laterally and from the sclerotome medially. There is no histological difference between cells of sclerotomic and dermatomic origin and the cells of the embryonic tissue constituting the clavicular anlage. Since the clavícula is not preformed in cartilage, it is regarded as a derivative of the cutis layer ("Hautfasernblatt").

Sternum

Anteriorly the two halves of the sternum have lengthened so that their anterior ends now lie ventro-medial to the postero-ventral procartilaginous fringes of the cartilagine coracoideae. At this stage the anlagen of the sternum seems to be continuous with the procartilaginous fringes of the cartilagine coracoideae, but the thin layer of embryonic connective tissue

separating these two structures, does not take up Bismarck-brown. As a result of the progressive downgrowth of the ventral borders of the cartilaginous coracoids, the anterior ends of the sternal anlagen now lie in the ventro-

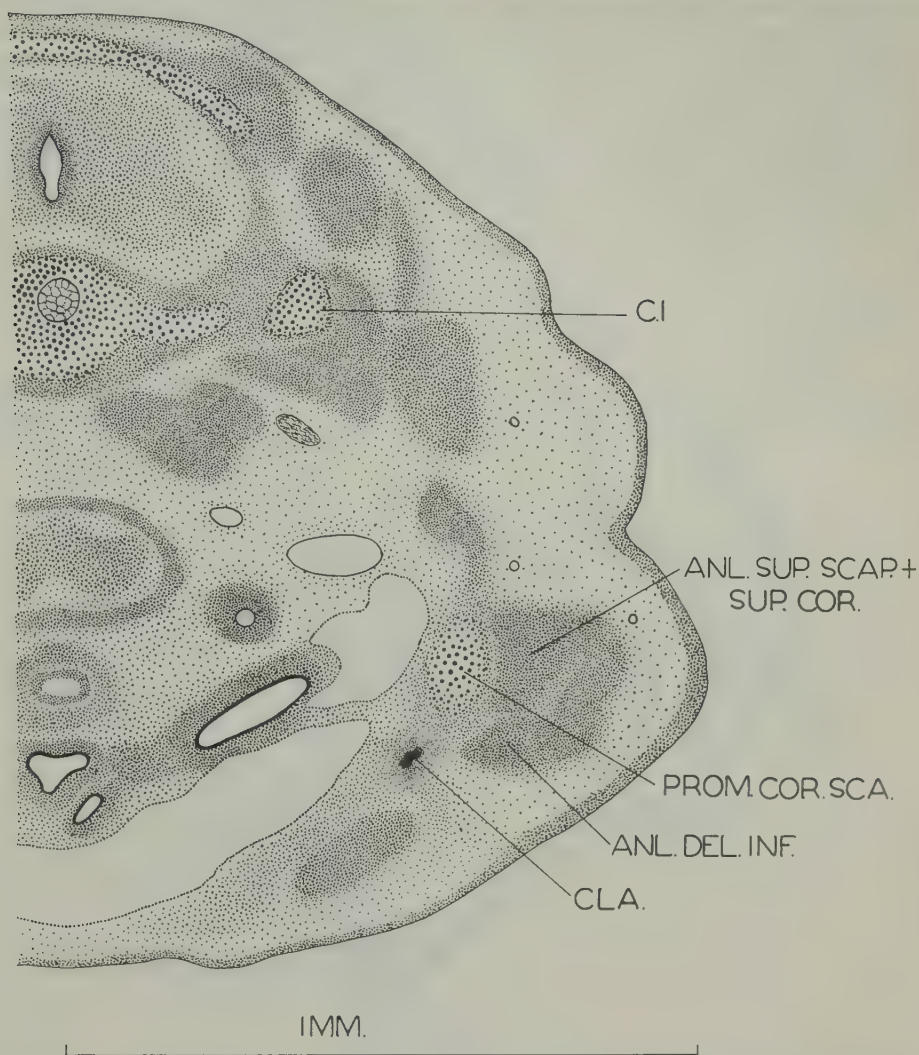


Figure 6.

Transverse section through the clavicle of an 18.5 mm. embryo. ANL. DEL. INF., anlage of the m. deltoideus inferior (m.d. clavicularis); ANL. SUP. SCAP. + SUP. COR., anlage of the m. suprascapularis + m. supracoracoideus (supracoracoscapularis); C.I., first cervical rib; CLA., clavicle; PROM. COR. SCA., prominentia coraco-scapularis.

lateral body-wall and therefore approach each other ventro-medially (Fig. 7). Chondrification has now set in, and the anterior part or praesternum is flattened, while the posterior part or meso- and xiphisternum is still in a procartilaginous or dense blastematous condition. The ventral parts of the first and second sternal ribs are procartilaginous and abut against the sternum. Posterior to the connexion of the second sternal rib the sternum, as well as the ventral end of the third thoracic rib, still consists of densely packed mesenchyme cells. There are no histological indications of the sternum arising from the sternal ribs. The sternal ribs become continuous with the sternal anlage when they are still in a blastematous condition, but the sternum and the sternal ribs chondrify separately.

E STAGE V

Length of embryo: 18.8 mm.

Shoulder-Girdle

The two halves of the girdle are considerably larger and occupy a more ventral position than in the previous stage. The shaft of the cartilago

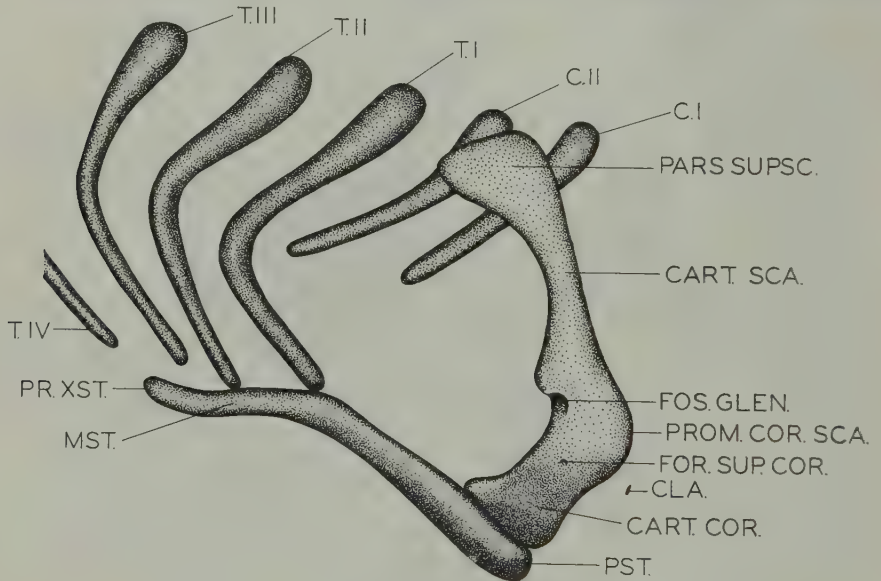


Figure 7.

Graphic reconstruction of the breast-shoulder apparatus of an 18.5 mm. embryo. X66.6. Norma lateralis. C.I. and C.II, cervical ribs; CART. COR., cartilago coracoidea; CART. SCA., cartilago scapularis; CLA., clavicula; FOR. SUP. COR., foramen for the n. supracoracoideus; FOS. GLEN., fossa glenoidalis; MST., mesosternum; PARS SUPSC., pars suprascapularis; PROM. COR. SCA., prominentia coraco-scapularis; PR. XST., processus xiphisternalis; PST., praesternum; T.I—T.III, thoracic ribs.

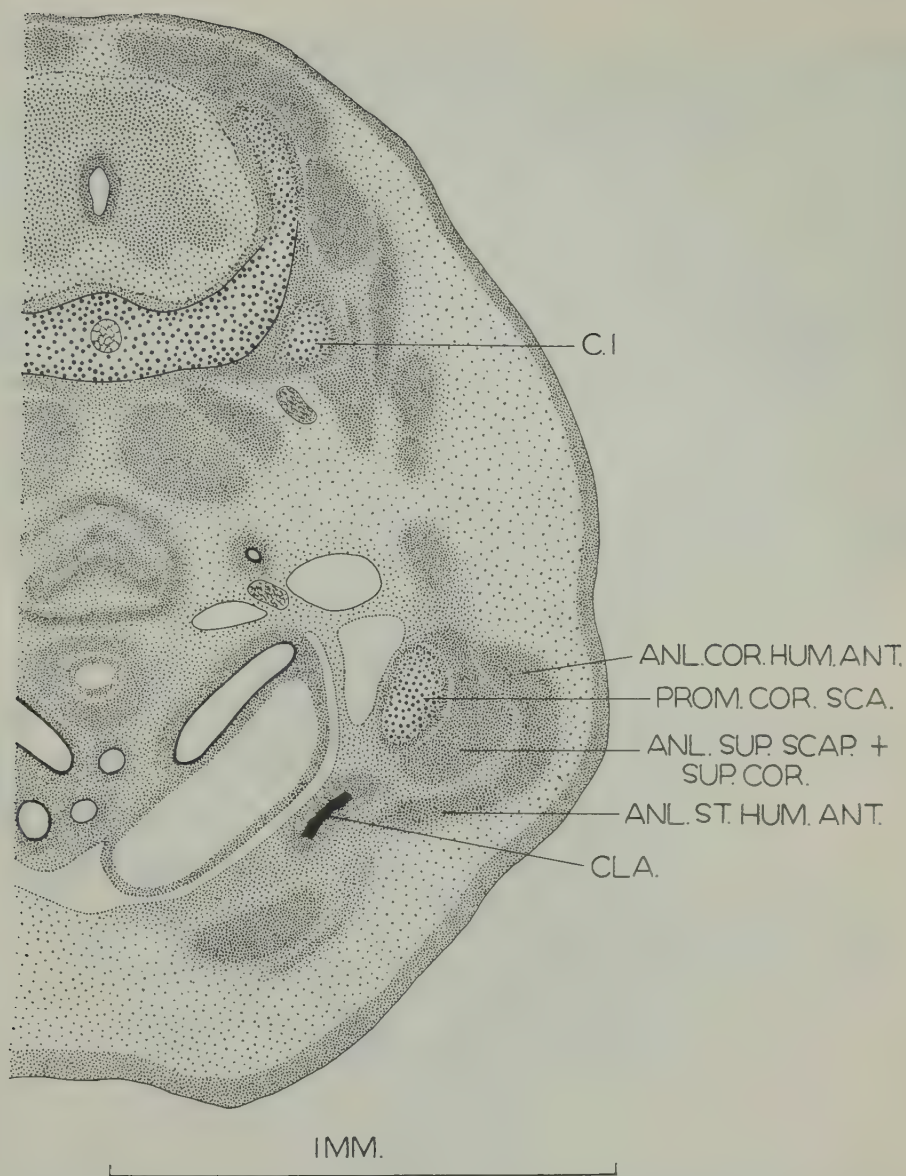


Figure 8.

Transverse section through the clavicle of an 18.8 mm. embryo. ANL. COR. HUM. ANT., anlage of the m. coraco-humeralis anterior; ANL. ST. HUM. ANT., anlage of the m. sterno-humeralis anterior; ANL. SUP. SCAP. + SUP. COR., anlage of the m. suprascapularis + m. supracoracoideus (supracoracoscapularis); C.I., first cervical rib; CLA., clavicula; PROM. COR. SCA., prominentia coraco-scapularis.

scapularis now possesses a well-developed perichondrium, and ventrally the chondrocytes are already highly hypertrophied. Perichondral ossification has set in, and a thin layer of perichondral bone now surrounds the shaft of the cartilago scapularis immediately dorsal to the prominentia coraco-scapularis which is more pronounced in this stage. Further reduction of the postero-ventral tuberosity, dorsal to the glenoid fossa, has taken place; but very little change has occurred in the cartilago suprascapularis. Further chondrification of the cartilago coracoidea has taken place, but in spite of the advanced degree of development, their ventral borders are still widely separated. Anteriorly the area between the caput humeri and the fossa glenoidalis is still occupied by dense embryonic connective tissue, but posteriorly resorption of this tissue marks the initiation of the synovial cavity. In contrast to the cartilago coracoidea, the proximal portion of the humerus is now surrounded by a well-developed perichondrium, and ossification has already commenced in the shaft of the humerus. Its chondrocytes are highly hypertrophied but marrow cavities are still absent.

The clavicle has lengthened in a medio-ventral direction and is solid. Dorso-laterally the embryonic connective tissue in which it is embedded is continuous with the undifferentiated perichondrium of the prominentia coraco-scapularis as well as with the ventral part of the m. deltoides inferior (Fig. 8).

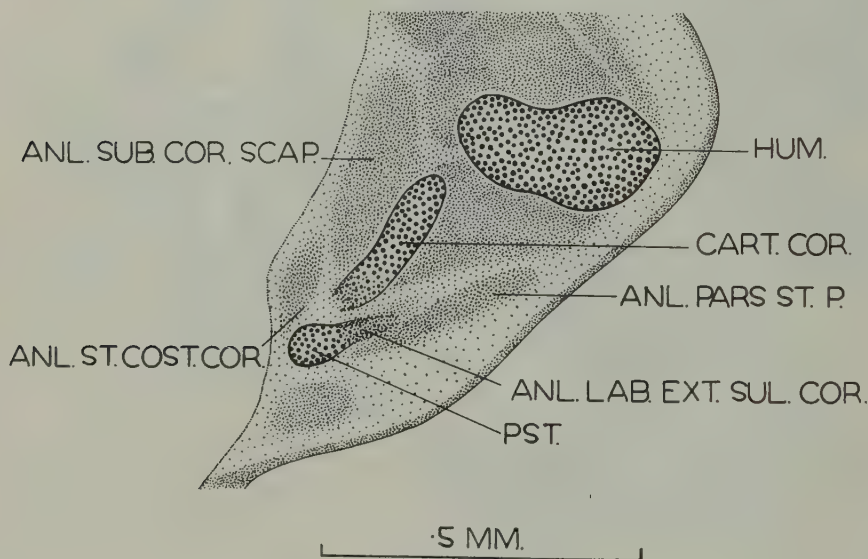


Figure 9.

Transverse section through the praesternum of an 18.8 mm. embryo. ANL. LAB. EXT. SUL. COR., anlage of the labium externum sulci coracoidei; ANL. PARS ST. P., anlage of the pars sternalis musculus pectoralis; ANL. ST. COST. COR., anlage of the m. sterno-costo-coracoideus; ANL. SUB. COR. SCAP., anlage of the m. subcoraco-scapularis; CART. COR., cartilago coracoidea; HUM., humerus; PST., praesternum.

Medio-ventrally this tissue is continuous with the embryonic tissue from which the anterior part of the m. pectoralis and other zonal muscles apparently arise.

The mesenchymatous tissue situated round the ventral borders of the two halves of the girdle has now become confluent ventrally. In the region of the praesternum, however, the two patches of tissue are still widely separated.

Sternum

The anterior ends of the two cartilaginous halves of the sternum have broadened considerably as a result of deposition of intercellular substance in the blastematous tissue medial to the anterior end of the sternal anlage, and in the tissue situated between the posterior end of the cartilago coracoidea

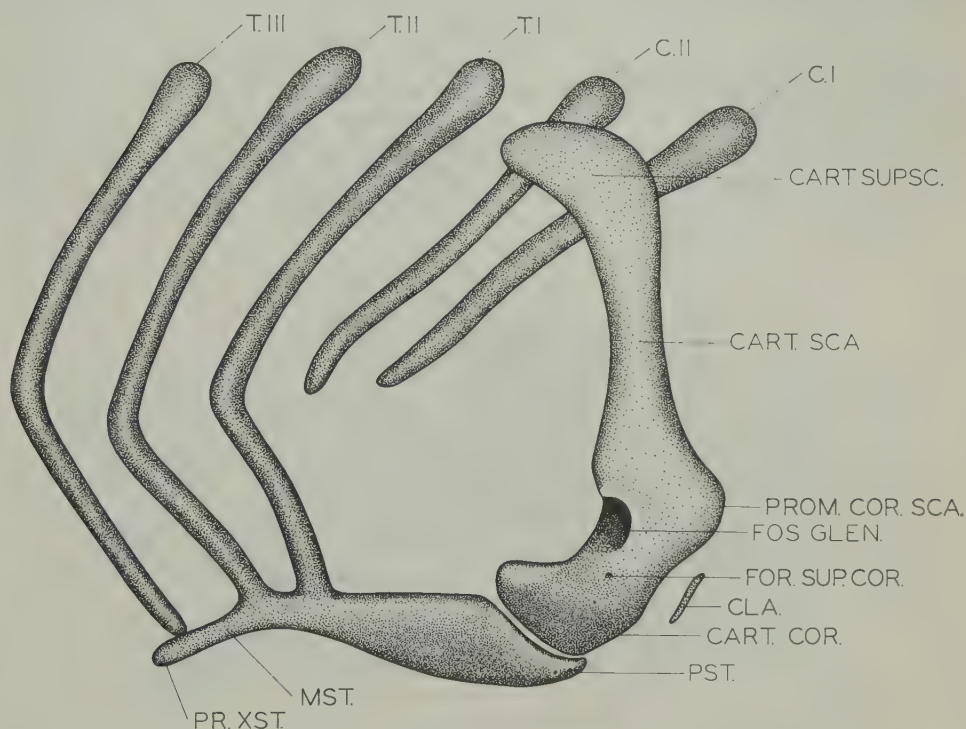


Figure 10.

Graphic reconstruction of the breast-shoulder apparatus of an 18.8 mm. embryo. X66.6. Norma lateralis. C.I and C.II, cervical ribs; CART. COR., cartilago coracoidea; CART. SCA., cartilago scapularis; CART. SUPSC., cartilago supra-scapularis; CLA., clavicula; FOR. SUP. COR., foramen for the n. supracoracoideus; FOS. GLEN., fossa glenoidalis; MST., mesosternum; PROM. COR. SCA., prominentia coraco-scapularis; PR. XST., processus xiphisternalis; PST., praesternum; T.I—T.III, thoracic ribs.

and the anlage of the pars sternalis musculi pectoralis. This blastematos tissue is continuous with the undifferentiated perichondrium of the sternal anlage (Fig. 9). Chondrification of the tissue in question results in the establishment of the lower lip of the sternal pouch: labium externum sulci coracoidei. The mesenchymatous tissue surrounding the two halves of the sternum is the mother tissue of the ventral aponeurosis, and therefore the latter is inevitably to be regarded as an important entity in the formation of the sternal mother tissue.

The first and second sternal ribs are now in synchondrotic continuity with the sternum (Fig. 10). Behind the junction of the second sternal rib the meso- and xiphisternum are procartilaginous, and extend up to a point immediately behind the ventral end of the third procartilaginous thoracic rib which at this stage abuts against the mesosternum.

F STAGE VI

Length of embryo: 19.5 mm.

Shoulder-Girdle

Little change has taken place in the girdle. The cartilagines coracoideae approach each other medio-ventrally so that their medial parts lie practically in the same horizontal plane. The shaft of the cartilago scapularis is partly

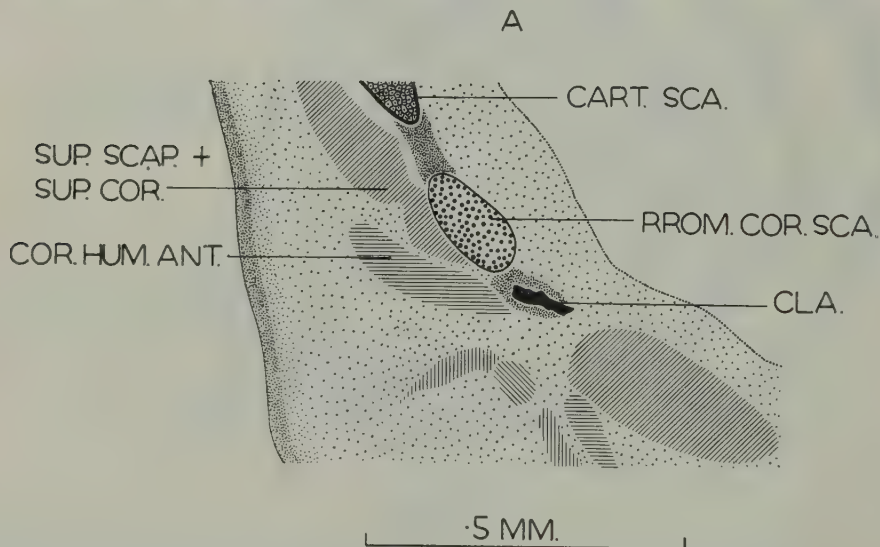


Figure 11a.

Transverse section through the anterior part of the clavicle of a 19.5 mm. embryo. CART. SCA., cartilago scapularis; CLA., clavicula; COR. HUM. ANT., m. coraco-humeralis anterior; PROM. COR. SCA., prominentia coraco-scapularis; SUP. SCAP. + SUP. COR., m. suprascapularis + m. supracoracoideus (supracoracoscapularis).

ossified perichondrally to form the scapula; but no sign of endochondral ossification occurs. The cartilago coracoidea possesses a well-developed but discontinuous perichondral capsule. Hypertrophied chondrocytes in the medial part of the cartilago coracoidea constitute the first indication of future ossification in this region. In the fossa glenoidalis the synovial cavity is well developed. A thick sheath of perichondral bone surrounds the shaft of the humerus; periosteal buds on this sheath indicate the beginning of endochondral ossification.

The clavicle has thickened and lengthened in a medio-ventral direction but lacks a marrow-cavity. Dorsally the periosteum of the clavicle is in syndesmotomic continuity with the undifferentiated perichondrium of the prominentia coraco-scapularis; ventrally it is in syndesmotomic continuity with the undifferentiated perichondrium of the anterior part of the labium externum sulci coracoidei of the sternum. The anterior portion of the m. deltoides inferior which, according to Fürbringer (1900), corresponds to the m. deltoides clavicularis of other *Lacertilia*, has divided into two bellies: a dorsal belly or m. coraco-humeralis anterior and a ventral belly or m. sterno-humeralis anterior, but the insertio on the pr. lateralis humeri remains single. The muscles in question are, however, quite distinct at their origins: the m. coraco-humeralis anterior arises from the anterior border and adjacent outer

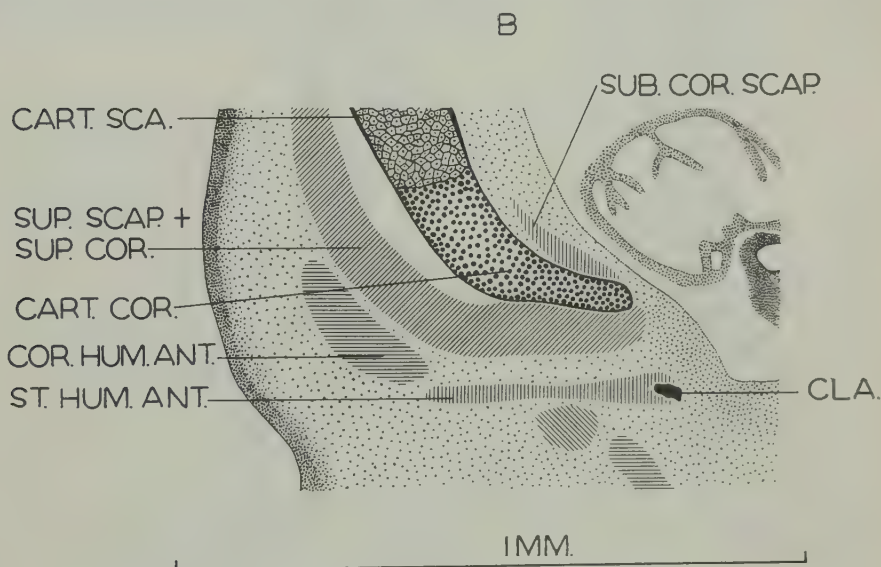


Figure 11b.

Transverse section through the posterior part of the clavicle of a 19.5 mm. embryo. CART. COR., cartilago coracoidea; CART. SCA., cartilago scapularis; CLA., clavicle; COR. HUM. ANT., m. coraco-humeralis anterior; ST. HUM. ANT., m. sterno-humeralis anterior; SUB. COR. SCAP., m. subcoraco-scapularis; SUP. SCAP. + SUP. COR., m. supra-scapularis + m. supracoracoideus (supracoracoscapularis).

surface of the cartilago coracoidea immediately anterior to the origo of the m. supracoracoideus as well as from the connective tissue between the clavícula and the prominentia coraco-scapularis and from the periosteum of the dorsal end of the clavícula itself (Fig. 11a). The m. sterno-humeralis anterior arises as a thin sheet of muscle along the posterior rim of the clavícula as well as from the connective tissue between the ventral end of the clavícula and the labium externum sulci coracoidei of the sternum (Fig. 11b).

The caps of embryonic tissue around the two halves of the sternum have now fused ventrally to form a broad continuous stretch of embryonic tissue

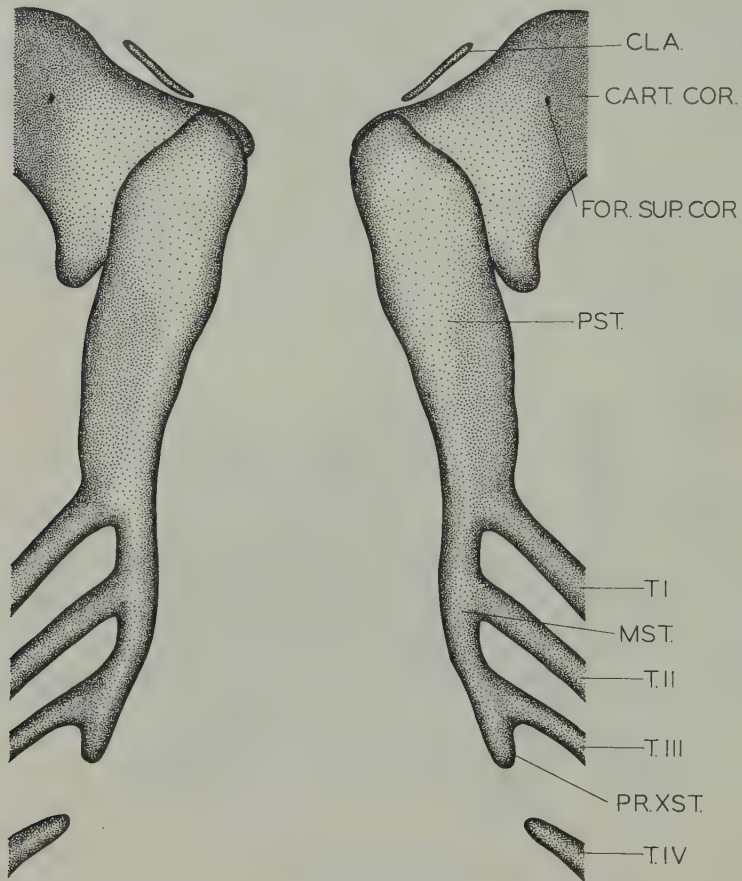


Figure 12.

Graphic reconstruction of the breast-shoulder apparatus of a 19.5 mm. embryo. X66.6. Norma ventralis. CART. COR., cartilago coracoidea; CLA., clavícula; FOR. SUP. COR., foramen for the n. supracoracoideus; MST., mesosternum; PR. XST., processus xiphisternalis; PST., praesternum; T.I—T.IV, thoracic ribs.

between the medial borders of the cartilagine coracoideae and the two halves of the sternum. It is impossible to say whether this tissue is of sclerotomic or of dermatomic origin, or a mixture of both.

Midventrally between the two halves of the sternum this tissue has become denser and is already extended posteriorly up to the niveau of the posterior ends of the two halves of the sternum. This intersternal formative tissue represents the anlage of the interclavicula.

Sternum

Midventrally the two halves of the sternum closely approach each other; the distance between their anterior tips being only $18\ \mu$. The labium externum sulci coracoidei of the sternum is now a well-developed structure in the anterior part of the praesternum, so that the praesternum now covers the medio-ventral fringe of the cartilago coracoidea (Fig. 12). In the posterior part of the praesternum the labium internum sulci coracoidei is seen developing in the same way as the labium externum: by means of intercellular matrix in the blastematous tissue between the medio-posterior border of the cartilago coracoidea and the anlage of the m. sterno-costo-coracoideus (Fig. 13). Although the labia sulci coracoidei develop in continuity with the undifferentiated perichondrium of the sternal anlage, they are essentially chondrifications of the mesenchymatous tissue belonging to the ventral aponeurosis.

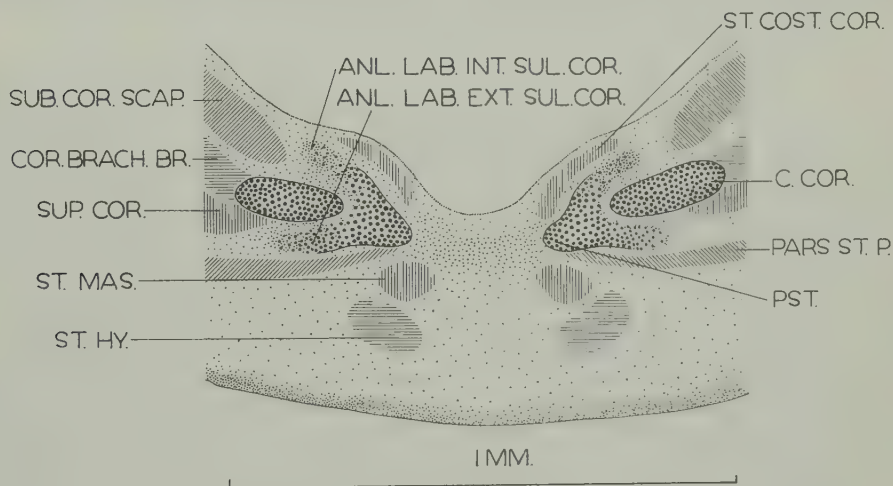


Figure 13.

Transverse section through the anterior coracoidal region of a 19.5 mm. embryo. ANL. LAB. EXT. SUL. COR., anlage of the labium externum sulci coracoidei; ANL. LAB. INT. SUL. COR., anlage of the labium internum sulci coracoidei; C. COR., cartilaginous fringe of the coracoid; COR. BRACH. BR., m. coraco-brachialis brevis; PARS ST. P., pars sternalis musculi pectoralis; ST. COST. COR., m. sterno-costo-coracoideus; ST. HY., m. sterno-hyoideus; ST. MAS., m. sterno-mastoideus; SUB. COR. SCAP., m. subcoraco-scapularis; SUP. COR., m. supracoracoideus.

Resorption of the embryonic connective tissue between the labium externum sulci coracoidei and the cartilago coracoidea indicates the initiation of a synovial cavity. The three pairs of sternal ribs are now in synchondrotic continuity with the two halves of the sternum, which latter is continued as the so-called xiphisternum behind the junction with the third pair of sternal ribs.

G STAGE VII

Length of embryo: 20.2 mm.

Shoulder-Girdle

The medial parts of the cartilagine coracoideae lie in the same horizontal plane and anteriorly they approach each other closely. The body of the cartilago coracoidea consists of highly hypertrophied chondrocytes and possesses a well-developed perichondrium in which the first signs of perichondral ossification already appear; its fringes still consist of procartilage. A thick sheath of perichondral bone surrounds the shaft of the scapula; internal to this sheath endochondral ossification has commenced. The cartilago suprascapularis remains unchanged. The dorsal parts of the two cervical and the three sternal ribs consist of a core of hypertrophied chondrocytes surrounded by a thick layer of perichondral bone.

In this stage the clavicular vestige attains its maximum size, measuring 0.33 mm. in length. Both its position and attachment are essentially the same as in the previous stage. The division of the *m. deltoideus inferior* into two bellies is more pronounced in this stage; the insertio on the *pr. lateralis humeri*, however, remains single. The dorsally situated *m. coraco-humeralis anterior* originates from the anterior border and adjacent outer surface of the cartilago coracoidea and from the connective tissue between the periosteum of the dorsal end of the clavícula and the perichondrium of the *prominentia coraco-scapularis*; only a few muscle fibres originate from the periosteum of the dorsal end of the clavícula. The *origo* of the ventrally situated *m. sterno-humeralis anterior* differs markedly from that of the previous stage in which the majority of the muscle fibres originate from the posterior rim of the clavícula. Only a few muscle fibres now arise from the clavícula itself, and from the connective tissue between the ventral end of the clavícula and the undifferentiated perichondrium of the outer rim of the labium externum sulci coracoidei. The majority of the muscle fibres arise from the undifferentiated perichondrium of the outer rim of the labium externum sulci coracoidei of the anterior part of the praesternum.

This stage is characterized by the appearance of the interclavícula. Midventrally the intersternal embryonic tissue has become more dense, and it now extends from a point immediately in front of the junction of the first pair of sternal ribs with the two halves of the sternum up to a point immediately behind the posterior ends of the xiphisternal processes. The interclavícula appears in transverse section as a diminutive patch of osseous tissue staining blue with azan; it is merely six consecutive 10 μ sections long (Fig. 14) and is embedded in the thickened intersternal tissue in the region of the junction of the first pair of sternal ribs with the sternum. Immediately anterior and

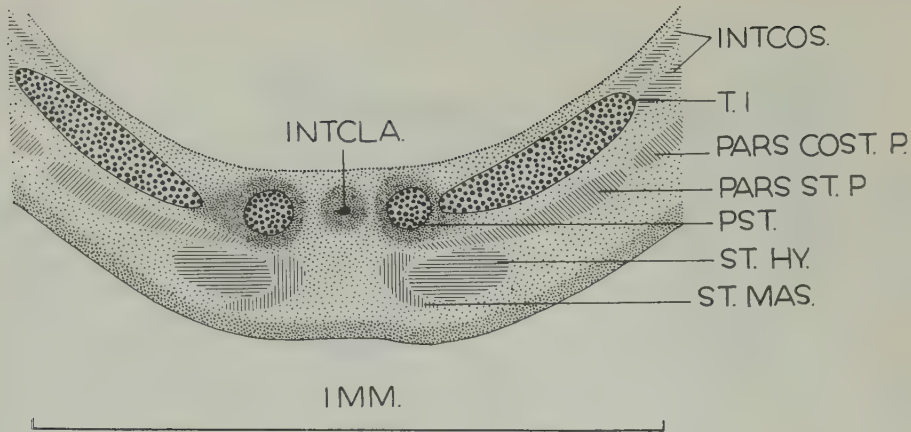


Figure 14.

Transverse section through the interclavicle of a 20.2 mm. embryo. INTCLA., interclavicle; INTCOS., intercostal musculature; PARS COST. P., pars costalis musculi pectoralis; PARS ST. P., pars sternalis musculi pectoralis; PST., praesternum; ST. HY., m. sterno-hyoideus; ST. MAS., m. sterno-mastoideus; T.I, first thoracic rib.

posterior to the interclavicle minute bony spicula may be observed in the intersternal tissue. The surrounding cells, however, are not clearly differentiated osteoblasts such as those in the immediate vicinity of the interclavicle itself. I have taken the precaution of cutting several additional parallel series through this region in order to ascertain the maximum size reached by the interclavicle during the embryonic development but I did not come across a single specimen in which the interclavicle is relatively larger. The bony spicula are a constant feature in embryos of this size. The origin of the intersternal formative tissue is not certain, since there is no demonstrable histological difference between cells derived from the cutis layer of the myotome and those originating from the sclerotome. The composite tissue in question is in histogenetic continuity with tissue of sclerotomic and of dermatomic origin. This view is supported by the circumstance that such tissue gives rise to the sternal mother tissue and later contributes to the lateral growth of the sternum itself, as well as to bony tissue which is not preformed in cartilage but develops in the same way as all derivatives of the cutis layer.

Sternum

The anterior ends of the two halves of the sternum have now fused; in the most anterior sections the praesternum appears as a dorso-ventrally flattened patch of cartilage, and in the following sections the anterior ends of the two halves of the sternum approach each other so closely as to have at this point a common perichondrium. The medial parts of the praesternum

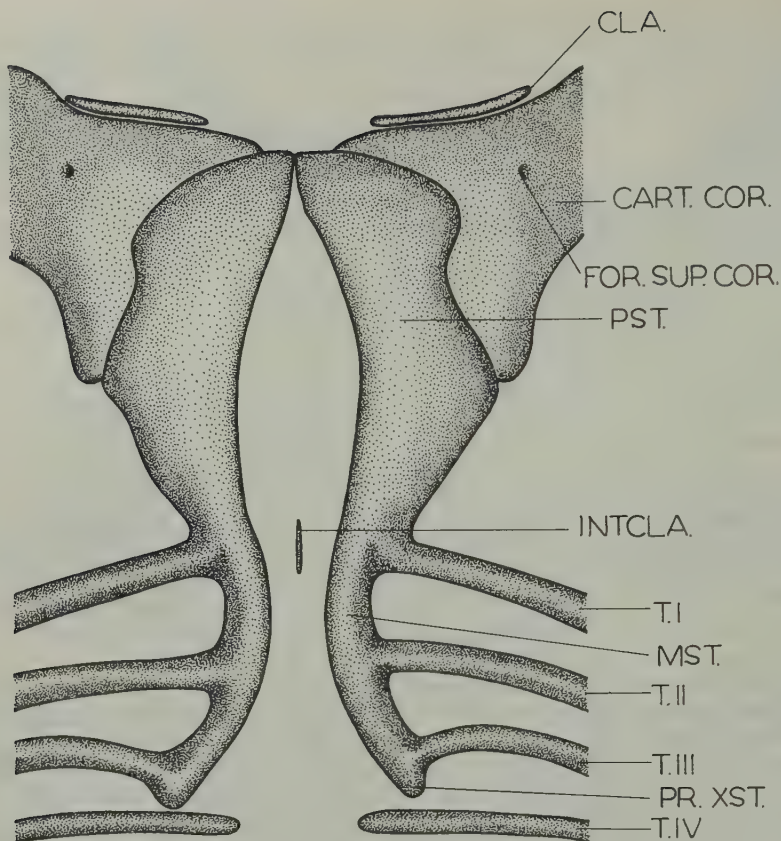


Figure 15.

Graphic reconstruction of the breast-shoulder apparatus of a 20.2 mm. embryo. X66.6. Norma ventralis. CART. COR., cartilago coracoidea; CLA., clavícula; FOR. SUP. COR., foramen for the n. supra-coracoideus; INTCLA., interclavícula; MST., mesosternum; PR. XST., processus xiphisternalis; PST., praesternum; T.I—T.IV, thoracic ribs.

are still widely separated, but in the region of the interclavícula they again approach each other medio-ventrally (Fig. 15). Although the labia sulci coracoidei are still procartilaginous, they are well-defined structures partially separated from the fringe of the cartilago coracoidea by means of a synovial cavity. The labium internum sulci coracoidei is continued posterior to the termination of the labium externum, and along its outer rim some of the intercostal muscles originate. In the posterior part of the praesternum and the anterior part of the mesosternum the first signs of perichondral ossification can already be observed.

H STAGE VIII

Length of embryo: 21.3 mm.

Shoulder-Girdle

The shoulder-girdle now has the adult appearance; the cartilago suprascapularis covers the upper parts of the two cervical and the first sternal ribs. It possesses a well-defined perichondrium which shows signs of perichondral ossification in that part adjoining the scapula; the chondrocytes are not hypertrophied. Ossification of the scapula is far advanced and in its shaft a large single marrow cavity is present. The body of the cartilago coracoidea is surrounded by a thick layer of perichondral bone but as yet no sign of endochondral ossification is evident. Anterior to the sternum the cartilaginous border of the right coracoid overlaps the left. This condition has received much attention from workers on the *Anura* and has been called "arcifery". It is interesting that such overlapping is not confined to *Amphibia*, but is apparently conditioned by the relative volume of the viscera encircled by the posterior parts of the coracoidal plates. They are syndesmotically connected with each other as well as with the anterior end of the sternum by means of dense connective tissue which is moreover continuous with the synovial membrane between the coracoids and the sternum.

Resorption of the osseous tissue of the clavícula has now set in so that the vestige is much smaller than in the previous stage. Strands of connective tissue on either side indicate the former positions of the dorsal and ventral ends, and they are continuous dorsally with the perichondrium of the prominentia coraco-scapularis and ventrally with the labium externum sulci coracoidei. Resorption of the clavícula has also affected the origo of the m. deltoides inferior; the m. coraco-humeralis anterior now largely originates from the anterior border of the cartilago coracoidea and adjoining area immediately anterior to the origo of the m. supracoracoideus. To a much lesser extent it also arises from the connective tissue between the dorsal end of the clavícula and the prominentia coraco-scapularis. The m. sterno-humeralis anterior arises partly from the ligament between the ventral end of the clavícula and the sternum, but the greater part now originates from the outer rim of the anterior part of the labium externum sulci coracoidei. The remains of the clavícula is thus embedded between the two bellies of the m. deltoides inferior in a strand of connective tissue situated between the sternum and the cartilago coracoidea.

Sternum

The two halves of the sternum have now fused anteriorly for a short distance and abut closely in the junctional region of the second pair of sternal ribs (Fig. 16). The two halves of the praesternum are still separated for most of their length, but the area in between is occupied by dense connective tissue which is continuous with the ventral aponeurosis of the muscoli pectorales. Complete resorption of the interclavícula has taken place, and the intersternal tissue now consists of dense connective tissue except in the region where the two halves of the mesosternum touch; at this point only a common

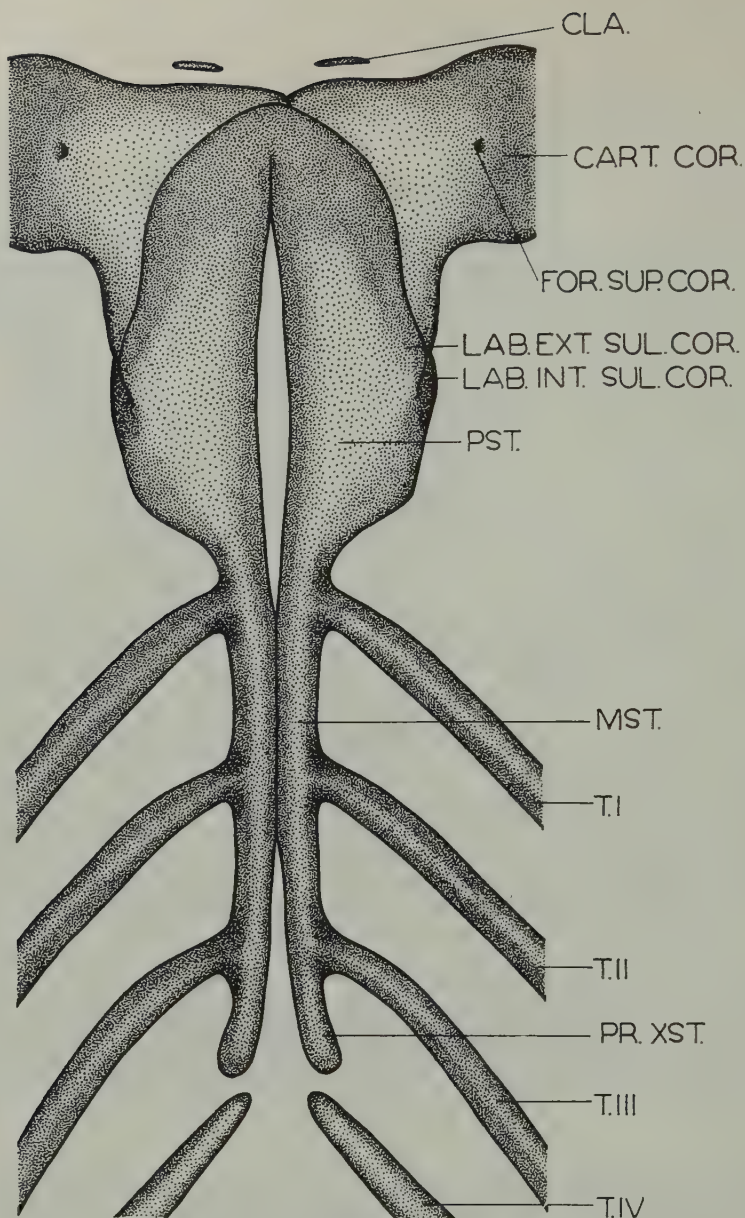


Figure 16.

Graphic reconstruction of the breast-shoulder apparatus of a 21.3 mm. embryo. X66.6. Norma ventralis. CART. COR., cartilago coracoidea; CLA., clavicula; FOR. SUP. COR., foramen for the n. supracoracoideus; LAB. EXT. SUL. COR., labium externum sulci coracoidei; LAB. INT. SUL. COR., labium internum sulci coracoidei; MST., mesosternum; PR. XST., processus xiphisternalis; PST., praesternum; T.I—T.IV, thoracic ribs.

perichondrium is discernable. Perichondral ossification of the mesosternum has already commenced and has also affected the junctional regions of the three pairs of sternal ribs.

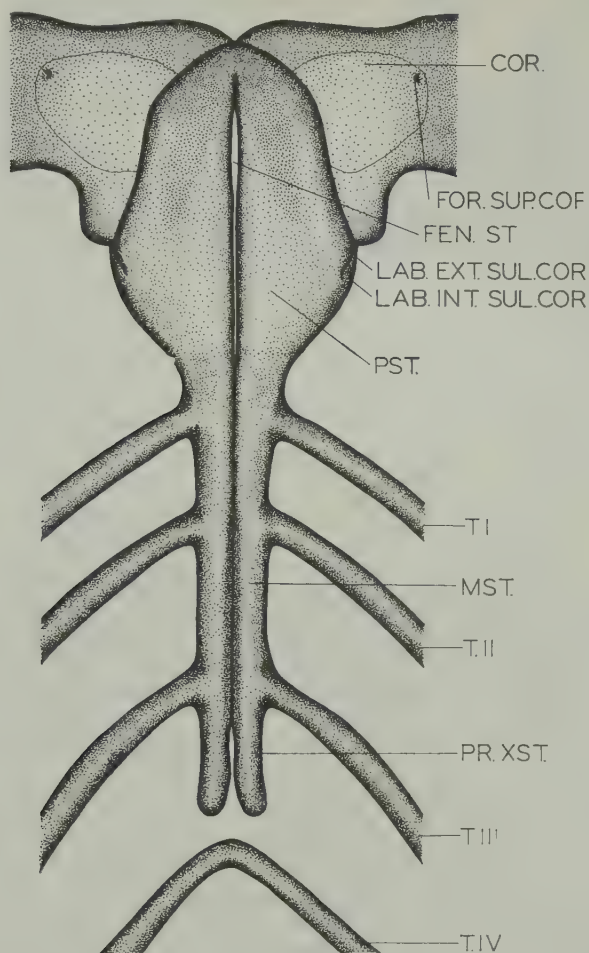


Figure 17.

Graphic reconstruction of the breast-shoulder apparatus of a 21.9 mm. embryo. X44.4. Norma ventralis. COR., coracoid; FEN. ST., fenestra sterni; FOR. SUP. COR., foramen for the n. supra-coracoideus; LAB. EXT. SUL. COR., labium externum sulci coracoidei; LAB. INT. SUL. COR., labium internum sulci coracoidei; MST., mesosternum; PR. XST., processus xiphisternalis; PST., praesternum; T.I—T.IV, thoracic ribs.

I STAGE IX

Length of embryo: 21.9 mm.

Shoulder-Girdle

Only a few minor changes in the shoulder-girdle have taken place, so that, except for increase in size, it does not differ markedly from the previous stage. Perichondral ossification of the cartilago suprascapularis has proceeded from the part bordering on the scapula, and it has affected practically the whole perichondrium of the cartilago suprascapularis. Periosteal buds on the thick layer of perichondral bone surrounding the central part of the coracoid indicate that endochondral ossification is about to commence. Where the perichondrium of the persistent cartilaginous fringes of the coracoid meets this layer of perichondral bone, it (the perichondrium) shows the first signs of ossification.

Resorption of the clavicle is now nearly completed so that the bone appears in only two consecutive 10μ sections. The ligament of connective tissue indicating the former position of the clavicle now occupies a more ventral position than in the previous stage. Resorption of the clavicle has not affected the origo of the m. deltoideus inferior to any further extent in this stage.

Sternum

The two halves of the sternum are now very closely applied to each other. Only the anterior ends of the two halves of the praesternum have fused completely, while their inner edges are separated by connective tissue (Fig. 17). The two halves of the mesosternum have not yet fused, so that the latter now consists of two bars of cartilage closely applied to each other. In the region between the junctions of the first and second pairs of sternal ribs they abut so closely that a single perichondrium is discernable between them. In intermediate stages fusion takes place in this region even before the posterior parts of the praesternum fuse. It would therefore appear that fusion of the two halves of the mesosternum spreads anteriorly and posteriorly from this region. In this stage the future xiphisternum still consists of two parallel bars of cartilage separated by connective tissue. Postero-ventral to the ends of these xiphisternal processes the ventral ends of the fourth pair of thoracic ribs meet.

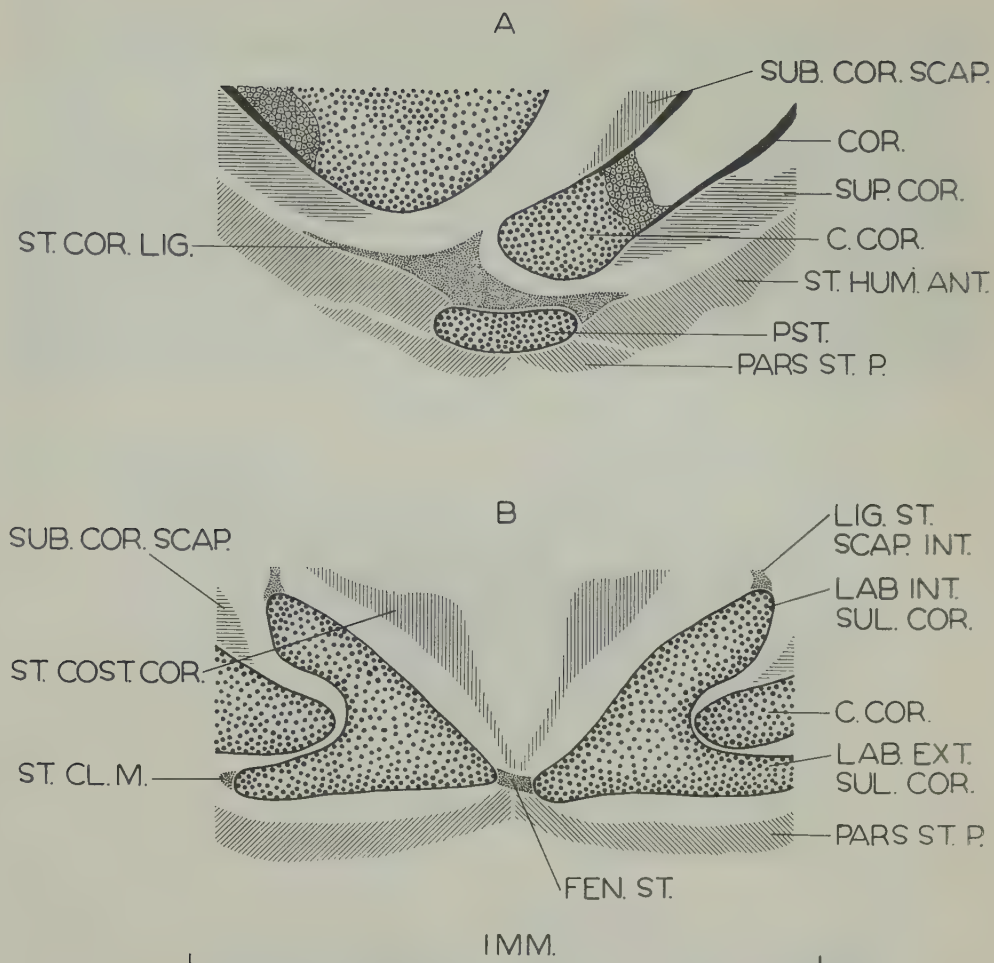
The degree of perichondral ossification of the mesosternum and sternal ribs does not differ very much from that in the previous stage, although perichondral ossification of the praesternum has now also commenced.

J STAGE X

Length of embryo: 27.0 mm.

Shoulder-Girdle

Very little histological differentiation of the shoulder-girdle has taken place, and consequently it does not differ very much from that described in



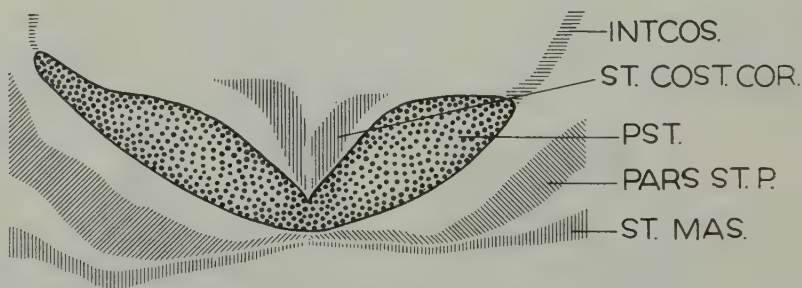
Figures 18a—f.

Transverse sections through the sternum of a 27.0 mm. embryo. C. COR., cartilaginous fringe of the coracoid; COR., coracoid; FEN. ST., fenestra sterni; INTCOS., intercostal musculature; L.A., linea alba; LAB. EXT. SUL. COR., labium externum sulci coracoidei; LAB. INT. SUL. COR., labium internum sulci coracoidei; LIG. ST. SCAP. INT., ligamentum sterno-scapulare internum; MST., mesosternum; PARS ST. P., pars sternalis musculi pectoralis; PST., praesternum; REC. ABD., m. rectus abdominis; ST. CL. M., m. sterno-cleido-mastoideus; ST. COR. LIG., sterno-coracoid ligament; ST. COST. COR., m. sterno-costo-coracoideus; ST. HUM. ANT., m. sterno-humeralis anterior; ST. HY., m. sterno-hyoideus; ST. MAS., m. sterno-mastoideus; SUB. COR. SCAP., m. subcoraco-scapularis; T.I and T.II, thoracic ribs; XST., xiphisternum.

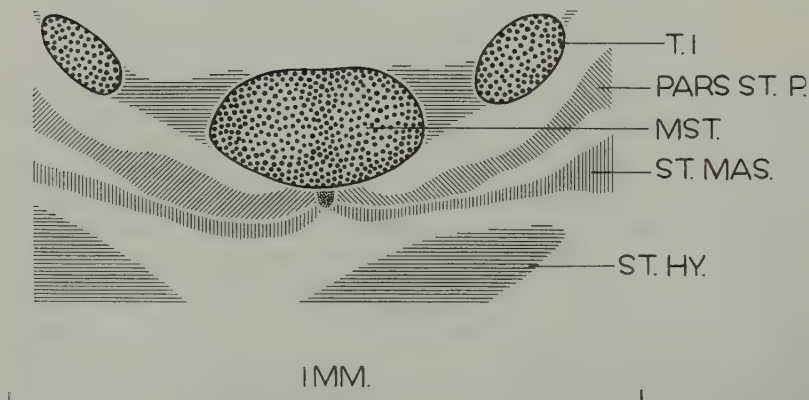
the two previous stages except for a marked increase in size. Endochondral ossification of the coracoid has set in, and a large central marrow cavity is now present. There is little progress in the perichondral ossification of the cartilaginous fringes of the coracoid.

The replacement of the clavicle by a strong ligament is now complete. The ligament stretches from the ventral part of the prominencia coraco-scapularis, runs obliquely downwards and is attached to the connective tissue lying between the two coracoids and the anterior part of the sternum. Further modification of the origines of the two bellies of the m. deltoideus inferior has also occurred: the m. coraco-humeralis anterior arises from the anterior border of the coracoid and the adjoining ventral part of the prominencia coraco-scapularis immediately posterior to the attachment of the sterno-coracoid ligament. The origo of the ventral belly, however, still differs from that of the adult but does not differ very much from that described for the

C



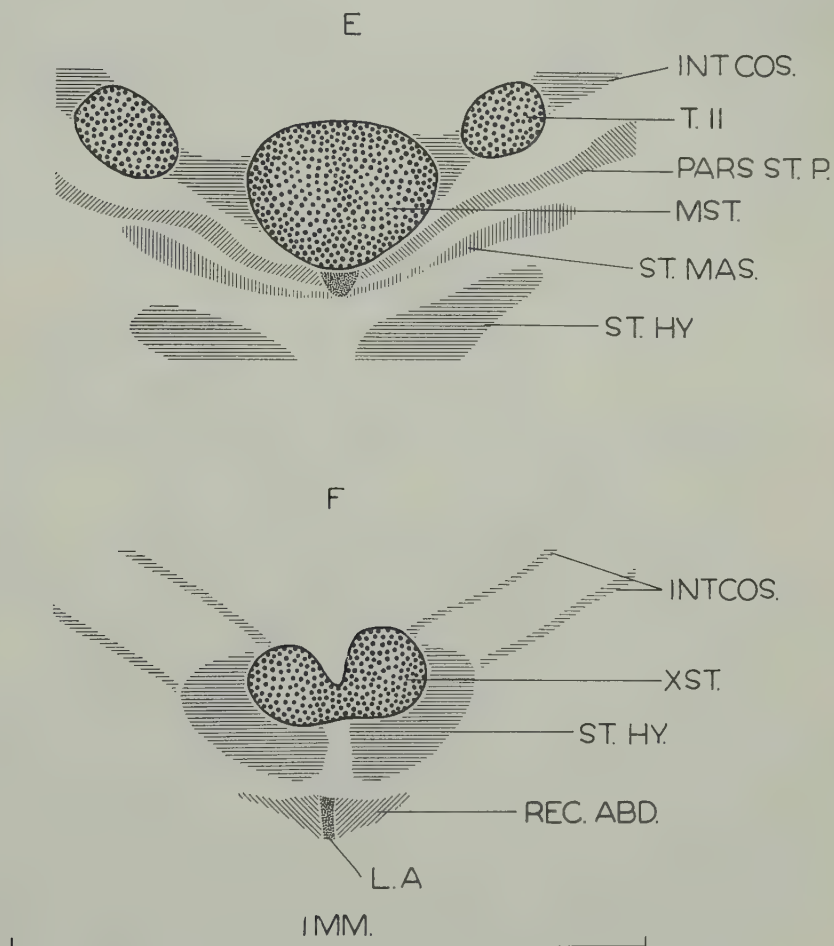
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21.3 mm. stage. Although the two bellies are now separated for most of their length, the insertio on the pr. lateralis humeri remains single.

Sternum

The two sternal rudiments have now fused to form the unpaired arrow-shaped sternum of the adult. The anterior and posterior parts of the praesternum have also completely fused, while the edges of the central parts remain separated to form a fenestra (Figs. 18a, b and c). This fenestra is closed by dense connective tissue which is ventrally continuous with the ventral aponeurosis of the partes sternales musculorum pectoralium and dorsally with the connective tissue between the mm. sterno-costo-coracoidei (Fig. 18b). Since these muscles are derivatives of the mm. abdominis recti, the tissue between them can only be regarded as that part of the linea alba



situated internal to the sternum. Immediately anterior and posterior to the fenestra sterni the inner edges of the two halves of the praesternum have not fused but are merely contiguous. The position of the fenestra sterni differs from individual to individual, but in most specimens it is situated somewhat anteriorly in the praesternum.

Complete fusion of the two halves of the mesosternum and xiphisternum has also taken place so that they now resemble a dorso-ventrally flattened rod (Fig. 18d and e) which is now relatively longer than in the previous stage. The part between the junctions of the second and third pair of sternal ribs and the xiphisternum shows the greatest increase in length. The paired origin of the sternum is still evident, however, since the xiphisternum is dorsally grooved in a cranio-caudal direction (Fig. 18f). The posterior end of the xiphisternum is dorso-ventrally flattened and usually fenestrated; the number of fenestrae varies from one to three, but occasionally a specimen is encountered in which fenestrae are totally absent.

The ventral ends of the fourth pair of thoracic ribs meet immediately postero-ventral to the posterior end of the xiphisternum, and they are now completely fused. There is no indication of a so-called "metasternum" such as Parker (1868) has described for *Chamaeleo vulgaris* and *C. pumilus* (*Microsaura pumila*).

Perichondral ossification of the sternum is much more advanced than in the previous stage; the entire sternum with the exception of the outer edges of the labia sulci coracoidei and the mid-line is covered by a thin discontinuous layer of perichondral bone. This also applies to the ventral cartilaginous parts of the three sternal ribs.

V THE ANATOMY OF THE ADULT BREAST-SHOULDER APPARATUS

Contributions to our knowledge of the breast-shoulder apparatus of the *Chamaeleontidae* were made by Rathke (1853), Stannius (1856), W. K. Parker (1868), Cope (1892), Siebenrock (1893) and Fürbringer (1876 and 1900).

Shoulder-Girdle

The shoulder-girdle of *Microsaura* does not closely resemble that of the more typical *Lacertilia* or even of the primitive chamaeleontid *Brookesia* as described by Siebenrock (1893); but agrees with that of *Chamaeleo* and *Chirotes* (*Amphisbaenidae*) (Parker, 1868). The adult shoulder-girdle of the different genera of the *Chamaeleontidae* all lack membrane bones.

In the young adult male investigated, the cartilago suprascapularis covers the dorsal parts of the two cervical and the first thoracic rib. It is a flat, relatively small cartilaginous structure differing from that of *Chamaeleo* and *Brookesia* inasmuch as it is entirely covered by a thin layer of perichondral bone. The scapula is a narrow, flattened bony rod, broadening dorsally where it passes into the suprascapular region. Ventrally it is even broader where it borders on the coracoid. This latter element is not entirely ossified but is fringed with persistent cartilage covered by a thin discontinuous layer of perichondral bone. It has no fenestrae, but near the scapula it is pierced by a foramen through which the n. supracoracoideus passes. Between the scapula and the coracoid there is a thin layer of cartilage continuous with the

cartilaginous lining of the glenoid fossa. At the anterior junction of the scapula and the coracoid each possesses an anterior bony process; the processes are covered with cartilage and form the *prominentia coraco-scapularis* (Fig. 19). Posteriorly both the scapula and the coracoid take part in the formation of the *fossa glenoidalis*.

The proximal portion of the humerus has three processes: the *caput humeri*, a *pr. lateralis* and a *pr. medialis*. The distal portion was not studied in detail.

There are five cervical vertebrae, the last two of which possess ribs. The cartilaginous ventral parts of these are very short and do not reach the sternum.

Sternum

Rathke (1853) distinguishes an anterior and a posterior portion of the sternum, although the entire sternum consists of a single piece. Parker (1868) named the anterior part the *manubrium sterni* or "*praesternum*" and the posterior part the "*mesosternum*". He applied the name "*xiphisternum*" to

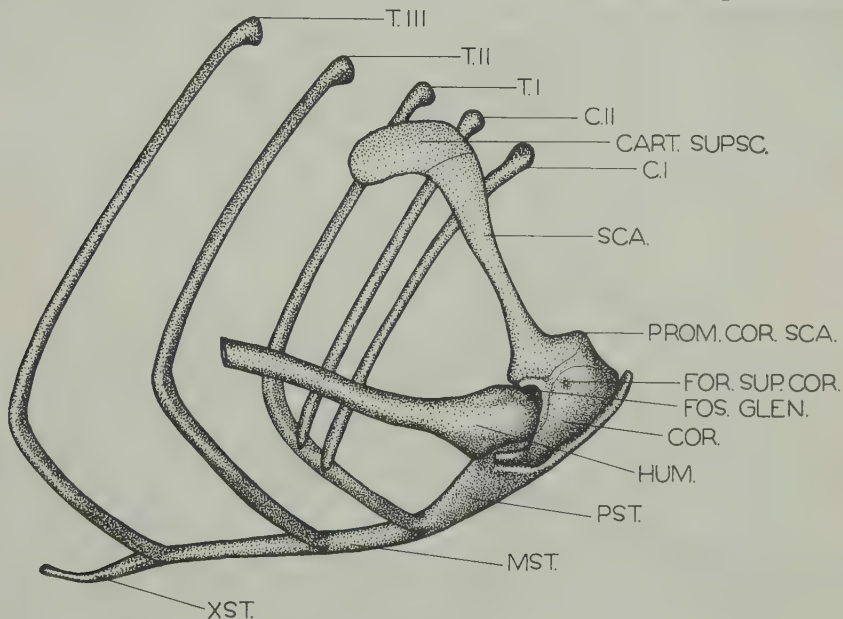


Figure 19.

Graphic reconstruction of the breast-shoulder apparatus of a young adult male. X6.6. Norma lateralis. C.I and C.II, cervical ribs; CART. SUPSC., cartilago suprascapularis; COR., coracoid; FOR. SUP. COR., foramen for the n. supracoracoideus; FOS. GLEN., fossa glenoidalis; HUM., humerus; MST., mesosternum; PROM. COR. SCA., prominentia coraco-scapularis; PST., praesternum; SCA., scapula; T.I—T.III, thoracic ribs; XST., xiphisternum.

that part of the sternum which is continued behind the junction of the third pair of sternal ribs with the sternum. Whether it is homologous with the human xiphisternum (B.N.A.) is uncertain.

The sternum of *Microsaura* consists of a single cartilage covered by a thin, discontinuous layer of perichondral bone except along the edges of the praesternum and along the mid-line. The first three pairs of thoracic ribs are in synchondrotic continuity with the sternum (Fig. 20). Immediately behind the junction of the first pair of sternal ribs the sternum is at its narrowest; the part anterior to the constriction is called the "praesternum", the posterior part the "mesosternum" and "xiphisternum". These names are adopted from Parker (1868) and are purely topographical and have no morphological significance. The outer surface of the praesternum is convex. The anterior end of the sternum has a blunt rounded end and broadens posteriorly to a point immediately behind the posterior ends of the coracoids. It then suddenly becomes narrow anterior to the first pair of sternal ribs. The antero-lateral edges of the praesternum are grooved to receive the ventral edges of the coracoids. The lower lip or labium externum sulci coracoidei projects further anteriorly, while the upper lip or labium internum sulci coracoidei is continued behind the termination of the labium externum. From

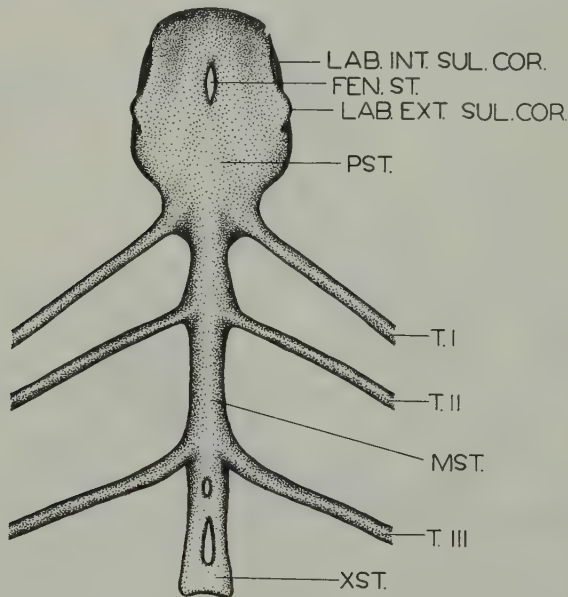


Figure 20.

Graphic reconstruction of the sternum of a young adult male. X6.6. Norma ventralis. FEN. ST., fenestra sterni; LAB. EXT. SUL. COR., labium externum sulci coracoidei; LAB. INT. SUL. COR., labium internum sulci coracoidei; MST., mesosternum; PST., praesternum; T.I—T.III, thoracic ribs; XST., xiphisternum.

the ridge so formed the intercostal musculature arises. The anterior ends of the coracoids and the sternum are joined together by means of dense connective tissue which is continuous with the synovial membrane between the coracoids and the sternum. In the mid-line of the anterior part of the sternum there is a fenestra sterni, which is closed by dense connective tissue. Only the first pair of sternal ribs is attached to the praesternum, and never during the ontogeny of the sternum is there any connexion with the cervical ribs.

Parker (1868) describes a deep, transverse notch in the sternum of *Chamaeleo vulgaris* immediately behind the junction of the first pair of sternal ribs with the sternum. Although the sternum of *Microsaura* narrows at this point, there is no deep notch. The mesosternum is a little shorter than the praesternum and is a slender cartilaginous rod slightly flattened dorso-ventrally. The second and third sternal ribs are in synchondrotic continuity with the mesosternum. The ventral parts of the sternal ribs are also covered by a thin layer of perichondral bone which is continuous with that of the sternum itself at the junctional regions.

The xiphisternum is that part of the sternum which is continued behind the third pair of sternal ribs with the mesosternum. It is dorso-ventrally flattened anteriorly and dorsally grooved in an antero-posterior direction posteriorly. Generally the xiphisternum is fenestrated; the number of fenestrae varies from one to three, but occasionally a specimen with a solid xiphisternum is found.

Immediately behind the xiphisternum the ventral ends of the fourth pair of thoracic ribs are synchondrotically connected. There is no connexion with the sternum, nor is there any indication of a supplementary sternal plate, the "metasternum", such as Parker (1868) describes for *Chamaeleo vulgaris* and *C. pumilus* (*Microsaura pumila*).

Musculature

Noteworthy papers on the musculature and particularly that of the general homologies of the tetrapod limb are those of Fürbringer (1873, 1874, 1876 and 1900), Gregory and Camp (1918), and Romer (1922, 1924 and 1944). For the sake of uniformity, the terminology employed in this paper is adopted from Romer (1922); Fürbringer's (1900) nomenclature is added in parenthesis. For a detailed account of the homologies of the fore-limb musculature of the *Reptilia* the reader is referred particularly to the works of Fürbringer (1900) and Romer (1922).

No attempt was made to include the nerves in the graphical reconstructions (Figs. 21-28), since it is impossible to trace nerve fibres through a plexus in order to determine their segmental origin in sections stained for the study of bone, cartilage and muscle.

The shoulder musculature of the *Chamaeleontidae* differs markedly from that of the "typical" *Lacertilia* because of the loss in the former of the dermal elements of the shoulder-girdle and the peculiar differentiation of the hyoid muscles. In this investigation my attention was confined to the origines and insertiones of the shoulder muscles and their relative positions to those adjacent to them.

The muscle normally called the *trapezius* (cucullaris) is small, thin and superficial, and originates from the dorsal fascia in the region of the processûs

spinosi of the third and, to a lesser extent, of the second thoracic vertebrae. It runs diagonally downwards and forwards across the antero-dorsal part of the m. latissimus dorsi and inserts on the anterior outer surface of the cartilago suprascapularis immediately posterior to the insertio of the dorsal belly of the m. levator scapulae superficialis.

The m. *sterno-cleido-mastoideus* arises from the lower part of the os squamosum and adjoining part of the os quadratum and inserts along the anterior edge of the labium externum sulci coracoidei between the ventral belly of the m. deltoideus inferior and m. supracoracoideus dorsally, and the pars sternalis musculi pectoralis ventrally. Near its insertio it crosses over the slender m. omo-hyoideus so that it is partly covered by and, in turn, partly covers the m. omo-hyoideus.

The m. *levator scapulae superficialis* is differentiated into two separate bellies; the m. levator scapulae superficialis superior and m. l. s. s. inferior (Fürbringer, 1900). The dorsally situated, inner m. levator scapulae super-

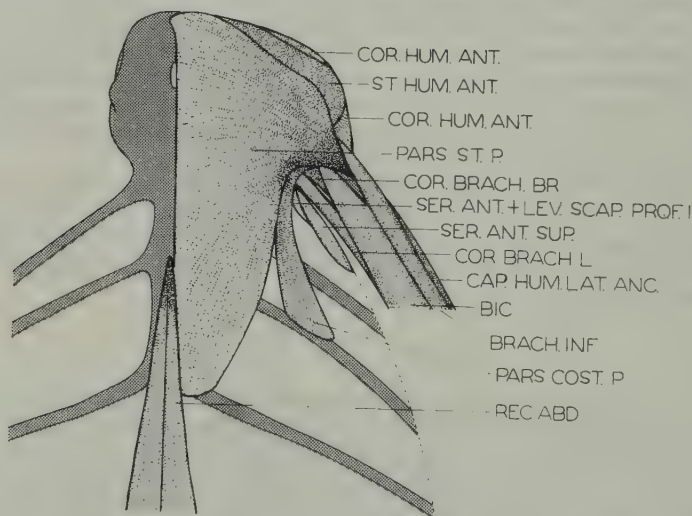


Figure 21.

Graphic reconstruction of the shoulder musculature of a young adult male. X5.5. Norma ventralis. BIC., m. biceps; BRACH. INF., m. brachialis inferior; CAP. HUM. LAT. ANC., lateral humeral head of the m. triceps; COR. BRACH. BR., m. coraco-brachialis brevis; COR. BRACH. L., m. coraco-brachialis longus; COR. HUM. ANT., m. coraco-humeralis anterior; PARS COST. P., pars costalis musculi pectoralis; PARS ST. P., pars sternalis musculi pectoralis; REC. ABD., m. rectus abdominis; SER. ANT. + LEV. SCAP. PROF. I., superficial layer of the m. serratus anterior et levator scapulae profundus; SER. ANT. SUP., m. serratus anterior superficialis; ST. HUM. ANT., m. sterno-humeralis anterior.

ficialis superior has a tendinous origo on the proximal portion of the pr. transversus of the first cervical vertebra; the outer, ventral belly or m. levator scapulae superficialis inferior has its origo on the distal portion of the pr. transversus of the same vertebra. The muscle fibres of both bellies diverge posteriorly to form two thin sheets; the dorsal belly inserts on the anterior rim and adjacent inner surface of the cartilago suprascapularis and to a much lesser extent on the dorsal part of the scapula. The ventral belly inserts along the anterior border of the central part of the scapula. The posterior part of the dorsal belly covers the deeper layer of the m. serratus anterior, and borders ventrally on the dorsal part of the m. scapulo-humeralis posterior; it runs dorsally to the m. trapezius. The ventral belly borders posteriorly on the m. suprascapularis and is partly covered posteriorly by the m. omo-hyoideus.

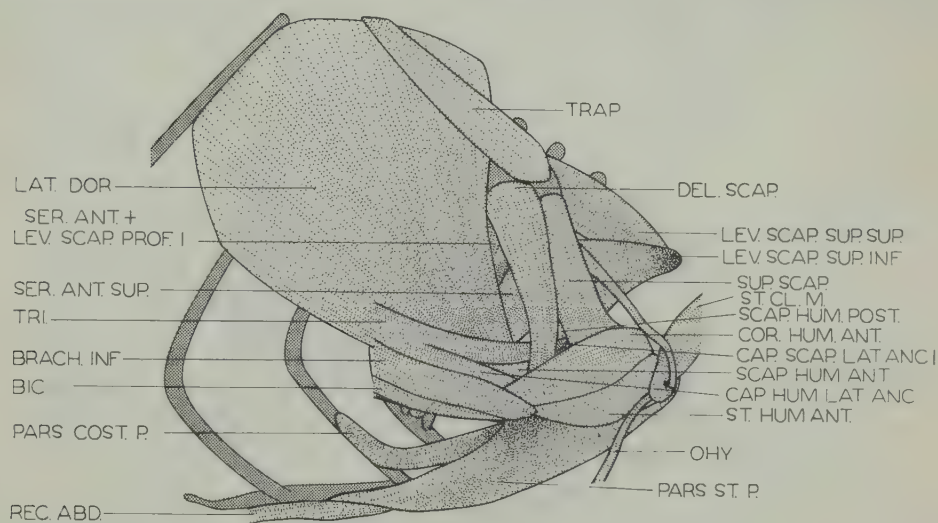


Figure 22.

Graphic reconstruction of the shoulder musculature of a young adult male. X5.5. Norma lateralis. BIC., m. biceps; BRACH. INF., m. brachialis inferior; CAP. HUM. LAT. ANC., lateral humeral head of the m. triceps; CAP. SCAP. LAT. ANC. I, superficial scapular head of the m. triceps; COR. HUM. ANT., m. coraco-humeralis anterior; DEL. SCAP., m. deltoides scapularis; LAT. DOR., m. latissimus dorsi; LEV. SCAP. SUP. INF., m. levator scapulae superficialis inferior; LEV. SCAP. SUP. SUP., m. levator scapulae superficialis superior; OHY., m. omo-hyoideus; PARS COST. P., pars costalis musculi pectoralis; PARS ST. P., pars sternalis musculi pectoralis; REC. ABD., m. rectus abdominis; SCAP. HUM. ANT., m. scapulo-humeralis anterior; SCAP. HUM. POST., m. scapulo-humeralis posterior; SER. ANT. + LEV. SCAP. PROF. I, superficial layer of the m. serratus anterior et levator scapulae profundus; ST. CL. M., m. sterno-cleido-mastoideus; ST. HUM. ANT., m. sterno-humeralis anterior; SUP. SCAP., m. suprascapularis; TRAP., m. trapezius; TRI., m. triceps.

The *m. serratus anterior superficialis* (*serratus superficialis*, Fürbringer) has its origins on the ventral parts of the two cervical ribs, runs diagonally in an antero-dorsal direction and inserts by means of a thin sheet of connective tissue along the posterior rim of the greater part of the scapula. Its anterior part covers the medial part of the *m. scapulo-humeralis posterior*, and its posterior part covers the anterior part of the *m. serratus anterior*. Posteriorly it is almost entirely covered by the *m. latissimus dorsi*, and anteriorly by the *m. deltoideus scapularis*.

The medial group of axial muscles moving the girdle was differently named by various workers: *m. levator scapulae et serratus profundus* (Für-

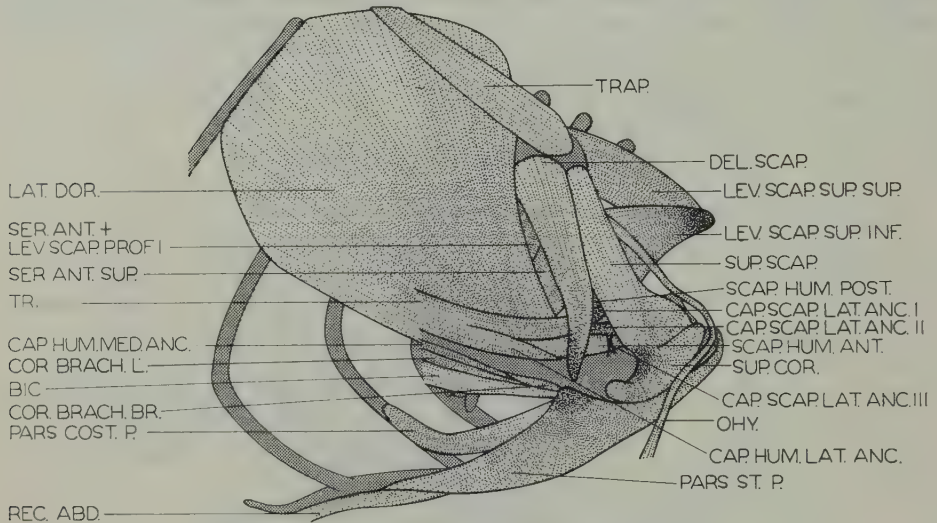


Figure 23.

The same as fig. 22 but with the *mm. brachialis inferior*, *coraco-humeralis anterior*, *sterno-cleido-mastoideus* and *sterno-humeralis anterior* removed. BIC., *m. biceps*; CAP. HUM. LAT. ANC., lateral humeral head of the *m. triceps*; CAP. HUM. MED. ANC., medial humeral head of the *m. triceps*; CAP. SCAP. LAT. ANC. I, superficial scapular head of the *m. triceps*; CAP. SCAP. LAT. ANC. II, deeper scapular head of the *m. triceps*; CAP. SCAP. LAT. ANC. III, humeral anchor of the deep scapular head of the *m. triceps*; COR. BRACH. BR., *m. coraco-brachialis brevis*; COR. BRACH. L., *m. coraco-brachialis longus*; DEL. SCAP., *m. deltoideus scapularis*; LAT. DOR., *m. latissimus dorsi*; LEV. SCAP. SUP. INF., *m. levator scapulae superficialis inferior*; LEV. SCAP. SUP. SUP., *m. levator scapulae superficialis superior*; OHY., *m. omohyoideus*; PARS COST. P., *pars costalis musculi pectoralis*; PARS ST. P., *pars sternalis musculi pectoralis*; REC. ABD., *m. rectus abdominis*; SCAP. HUM. ANT., *m. scapulo-humeralis anterior*; SCAP. HUM. POST., *m. scapulo-humeralis posterior*; SER. ANT. + LEV. SCAP. PROF. I, superficial layer of the *m. serratus anterior et levator scapulae profundus*; SER. ANT. SUP., *m. serratus superficialis*; SUP. COR., *m. supracoracoideus*; SUP. SCAP., *m. suprascapularis*; TRAP., *m. trapezius*; TRI., *m. triceps*.

bringer, 1900), m. serratus anterior and levator scapulae profundus (Romer, 1922) and the anterior part of the m. serratus magnus (Ribbing, 1938). In *Microsaura* this group closely resembles that of *Chamaeleo vulgaris* as described by Fürbringer (1900). It has differentiated into two layers, the outer of which is not completely separated from the m. serratus anterior superficialis. The upper layer has its origo on the ventral parts of the cervical ribs immediately dorsal to the origo of the m. serratus anterior superficialis and from the dorsal part of the first sternal rib. The ventral border of the muscle has a jagged appearance where it arises as two incompletely differentiated origines which soon converge. It runs antero-dorsally and inserts on the inner surface of the cartilago suprascapularis and adjoining area of the scapula. It covers the intercostal musculature and the postero-dorsal part of the m. scapulo-humeralis posterior. The muscle is covered by the m. latissimus

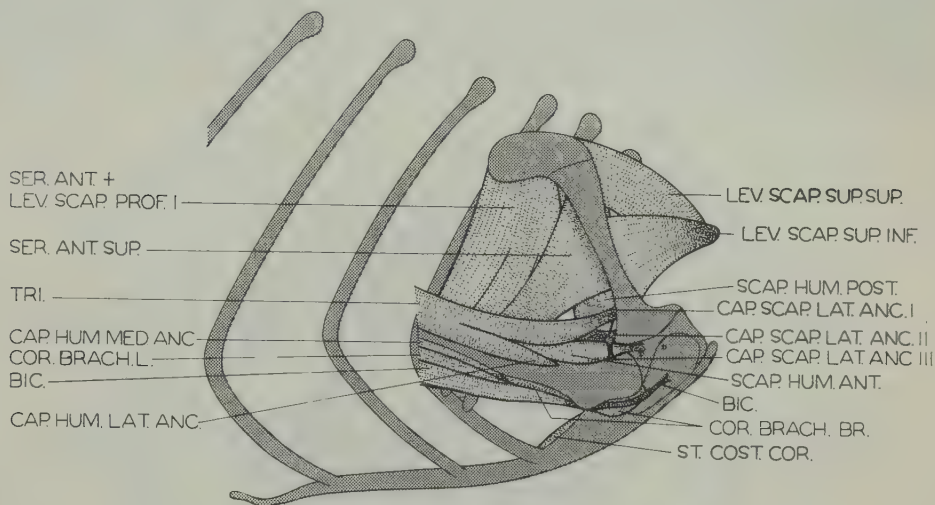


Figure 24.

The same as fig. 23 but with the mm. deltoides scapularis, latissimus dorsi, omo-hyoideus, pectoralis, rectus abdominis, suprocoracoideus, suprascapularis and trapezius removed. BIC., m. biceps; CAP. HUM. LAT. ANC., lateral humeral head of the m. triceps; CAP. HUM. MED. ANC., medial humeral head of the m. triceps; CAP. SCAP. LAT. ANC. I, superficial scapular head of the m. triceps; CAP. SCAP. LAT. ANC. II, deeper scapular head of the m. triceps; CAP. SCAP. LAT. ANC. III, humeral anchor of the deep scapular head of the m. triceps; COR. BRACH. BR., m. coraco-brachialis brevis; COR. BRACH. L., m. coraco-brachialis longus; LEV. SCAP. SUP. INF., m. levator scapulae superficialis inferior; LEV. SCAP. SUP. SUP., m. levator scapulae superficialis superior; SCAP. HUM. ANT., m. scapulo-humeralis anterior; SCAP. HUM. POST., m. scapulo-humeralis posterior; SER. ANT. + LEV. SCAP. PROF. I, superficial layer of the m. serratus anterior et levator scapulae profundus; SER. ANT. SUP., m. serratus anterior superficialis; ST. COST. COR., m. sterno-costo-coracoideus; TRI., m. triceps.

dorsi, m. serratus anterior superficialis and the m. deltoides scapularis. The deeper layer is a small, thin muscle originating from the upper part of the first cervical rib; it runs in an antero-posterior direction and inserts on the postero-dorsal, inner surface of the cartilago suprascapularis. It is covered by the dorsal part of the outer layer, the dorsal part of the m. scapulo-humeralis posterior and the posterior part of the m. levator scapulae superficialis superior.

The m. *sterno-costo-coracoideus* (sterno-coracoideus internus profundus) is situated internal to the sternum. Mid-ventrally the two muscles have given origin to an aponeurosis which is continuous with the connective tissue closing the fenestra sterni, and with the perichondrium of the unossified mid-line of the sternum. The muscle fibres insert mainly on the outer rim of the praesternum, but a few fibres also arise from the ventral ends of the first pair of sternal ribs. Anteriorly the fibres converge and terminate in a tendon inserting on the inner surface of the coracoid, antero-medial to the foramen for the n. suprascapularis. Medially the anterior part of the muscle is covered by the m. subcoraco-scapularis.

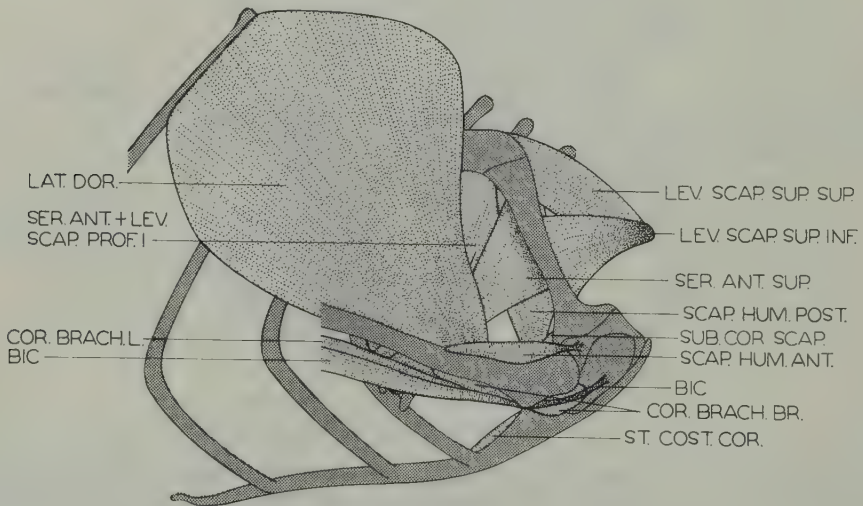


Figure 25.

The same as fig. 24 but with the m. triceps removed and the m. latissimus dorsi added. BIC., m. biceps; COR. BRACH. BR., m. coraco-brachialis brevis; COR. BRACH. L., m. coraco-brachialis longus; LAT. DOR., m. latissimus dorsi; LEV. SCAP. SUP. INF., m. levator scapulae superficialis inferior; LEV. SCAP. SUP. SUP., m. levator scapulae superficialis superior; SCAP. HUM. ANT., m. scapulo-humeralis anterior; SCAP. HUM. POST., m. scapulo-humeralis posterior; SER. ANT. + LEV. SCAP. PROF. I., superficial layer of the m. serratus anterior et levator scapulae profundus; SER. ANT. SUP., m. serratus anterior superficialis; ST. COST. COR., m. sterno-costo-coracoideus; SUB. COR. SCAP., m. subcoraco-scapularis.

Microsaura lacks a m. sterno-costo-scapularis, but medial to the m. subcoraco-scapularis there is a thin, strong ligament, the ligamentum sterno-scapulare internum (Fürbringer, 1900), running from the posterior part of the labium externum sulci coracoidei immediately anterior to the intercostal muscles to a point on the scapula well above its border with the coracoid.

The m. *pectoralis* is a large muscle entirely covering the sternum ventrally. It is underlain by the hyoid muscles which have their origines on the posterior part of the sternum. It is differentiated into two bellies: a pars sternalis and a pars costalis. The two partes sternales form a ventral aponeurosis which is continuous with the ventral aponeurosis of the m. sterno-mastoideus anteriorly and the m. sterno-hyoideus posteriorly. This composite ventral aponeurosis is histologically continuous with the perichondrium of the unossified mid-line of the sternum and with the linea alba between the mm. recti abdominis which terminate at the junction of the second pair of sternal ribs with the sternum. Anteriorly the two partes sternales musculorum pectoralium overlap, while posteriorly they are separated by the mm. recti abdominis. The pars costalis has its origo on the ventral part of the second

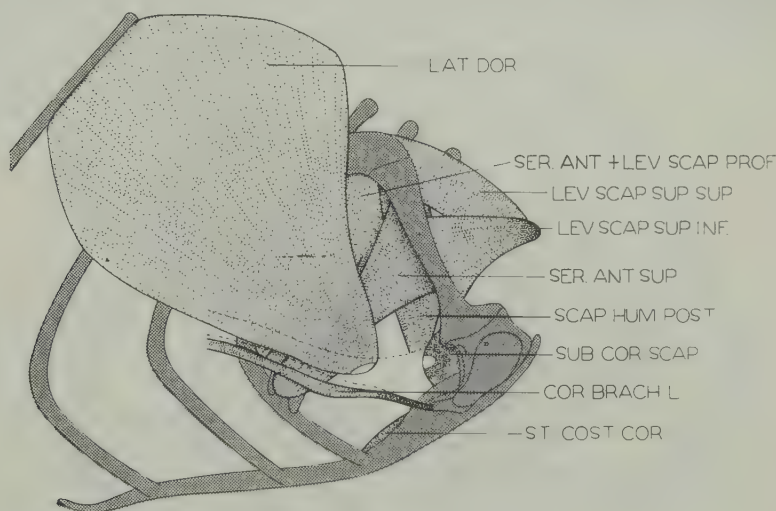


Figure 26.

The same as fig. 25 but with the humerus and the mm. biceps, coraco-brachialis brevis and scapulo-humeralis anterior removed. COR. BRACH. L., m. coraco-brachialis longus; LAT. DOR., m. latissimus dorsi; LEV. SCAP. SUP. INF., m. levator scapulae superficialis inferior; LEV. SCAP. SUP. SUP., m. levator scapulae superficialis superior; SCAP. HUM. POST., m. scapulo-humeralis posterior; SER. ANT. + LEV. SCAP. PROF. I, superficial layer of the m. serratus anterior et levator scapulae profundus; SER. ANT. SUP., m. serratus anterior superficialis; ST. COST. COR., m. sterno-costo-coracoideus; SUB. COR. SCAP., m. subcoraco-scapularis.

sternal rib, and at this point is quite distinct from the pars sternalis. The muscle fibres of both converge towards their insertiones on the pr. lateralis humeri between the m. brachialis, m. supracoracoideus and m. biceps. The pars costalis inserts distal to the pars sternalis by means of a tendon which is continuous with a sheath of connective tissue surrounding the tendon of the m. biceps where it passes over the tuberculum mediale. Anteriorly the pars sternalis covers the insertiones of the m. sterno-cleido-mastoideus, m. sterno-humeralis anterior and m. supracoracoideus. Near its insertio the m. pectoralis s. lat. covers the m. coraco-brachialis brevis and the proximal portions of the m. biceps and m. coraco-brachialis longus.

In *Chamaeleo* and *Brookesia* the m. supracoracoideus of other *Lacertilia* has differentiated into two bellies. Fürbringer (1900), therefore, calls it a m. supracoracoscapularis consisting of two more or less separate bellies: a ventrally situated m. *supracoracoideus* and a m. *suprascapularis*. In *Microsaura* the two bellies are not completely separated and have a common insertio on the proximal part of the pr. lateralis humeri, but they are quite distinct at their origines. The m. supracoracoideus is a broad muscle with

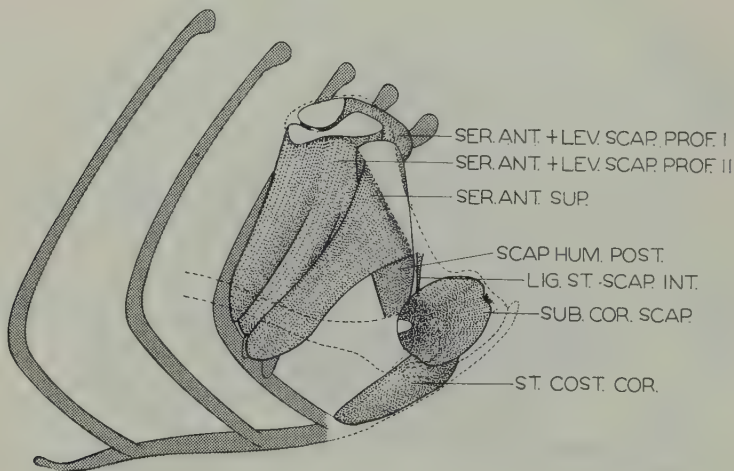


Figure 27.

The same as fig. 26 but with the humerus, part of the shoulder-girdle and the mm. coraco-brachialis longus, latissimus dorsi and levator scapulae superficialis removed. LIG. ST. SCAP. INT., ligamentum sterno-scapulare internum; SCAP. HUM. POST., m. scapulo-humeralis posterior; SER. ANT. + LEV. SCAP. PROF. I, superficial layer of the m. serratus anterior et levator scapulae profundus; SER. ANT. + LEV. SCAP. PROF. II, deeper layer of the m. serratus anterior et levator scapulae profundus; SER. ANT. SUP., m. serratus anterior superficialis; ST. COST. COR., m. sterno-costo-coracoideus; SUB. COR. SCAP., m. subcoraco-scapularis.

origo on the anterior, outer surface of the coracoid immediately posterior to the origo of the m. coraco-humeralis anterior. Ventro-laterally it covers the origines of the m. biceps and m. coraco-brachialis brevis. It is covered anteriorly by the m. deltoides inferior and posteriorly by the m. pectoralis. The m. suprascapularis has its origo on the antero-lateral surface of the scapula and thus lies adjacent to the anterior border of the m. deltoides scapularis. Ventrally it covers the origo of the m. scapulo-humeralis anterior and the scapular origines of the m. triceps, while it is covered in turn by the dorsal part of the m. deltoides inferior.

These muscles are innervated by the same nerve: the n. supratoracoides. Immediately after emerging from the foramen in the coracoid it divides into three small nerves: a ventral ramus to the m. supratoracoides, a dorsal to the m. suprascapularis and a smaller nerve which, after traversing the m. supratoracoides, runs between the m. deltoides inferior and the m. pectoralis to the skin in the coracoidal region.

The m. *coraco-brachialis brevis* is a short muscle on the ventral side of the humerus. It has a broad origo on the outer surface of the coracoid ventral to the fossa glenoidalis and inserts on the shaft of the humerus somewhat distal to the origo of the medial humeral head of the m. triceps. Anteriorly it lies between the m. supratoracoides and the m. subcoraco-

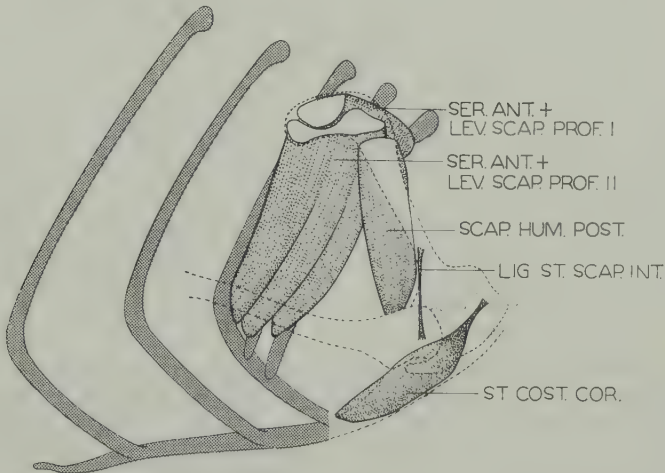


Figure 28.

The same as fig. 27 but with the mm. serratus anterior superficialis and subcoraco-scapularis removed. LIG. ST. SCAP., INT., ligamentum sterno-scapulare internum; SCAP. HUM. POST., m. scapulo-humeralis posterior; SER. ANT. + LEV. SCAP. PROF. I, superficial layer of the m. serratus anterior et levator scapulae profundus; SER. ANT. + LEV. SCAP. PROF. II, deeper layer of the m. serratus anterior et levator scapulae profundus; ST. COST. COR., m. sterno-costo-coracoides.

scapularis. Distally it is covered by the tendons of the m. biceps and m. coraco-brachialis longus and by the m. pectoralis s. lat.

The m. *coraco-brachialis longus* is a long, thin muscle with a tendinous insertio on the posterior cartilaginous end of the coracoid; distally it lies medio-ventral to the m. coraco-brachialis brevis. In the middle of the upper arm it runs between the m. biceps ventrally and the medial humeral head of the m. triceps dorsally and inserts on the distal part of the humerus.

The m. *biceps* (biceps brachii) has a tendinous origo on the outer surface of the coracoid and inserts on the radius and ulna. At its origo it is covered by the m. supracoracoideus, and proximally it lies between this muscle and the m. subcoraco-scapularis. Ventro-medial to the proximal part of the humerus, the tendon runs in a sheath of connective tissue, the sulcus bicipitalis, which is continuous with the insertio of the m. pectoralis. Proximally it covers the m. coraco-brachialis brevis and is covered by the m. pectoralis. The muscle is continued along the ventral surface of the humerus between the m. brachialis and the m. coraco-brachialis longus; distally it is united with the m. brachialis.

The m. *brachialis* (brachialis inferior) is a well-developed muscle situated ventro-laterally on the upper arm. It arises from the proximal surface of the humerus between the insertiones of the m. pectoralis and m. deltoideus inferior, and is continued between the m. biceps and the lateral humeral head of the m. biceps and the lateral humeral head of the m. triceps to the lower arm where it inserts on the radius and ulna.

The m. *latissimus dorsi* is a thin, broad muscle of the thorax arising from the dorsal fascia and from the processûs spinosi of the first three thoracic vertebrae as well as from the dorsal part of the fourth thoracic rib. The muscle fibres converge and, after passing medial to the scapular heads of the m. triceps, insert on the humerus between the m. scapulo-humeralis anterior and m. coraco-brachialis brevis. The fibres arising from the fourth thoracic rib insert proximal to the rest of the muscle. The m. latissimus dorsi covers the posterior parts of the m. serratus anterior superficialis and m. serratus anterior and the cartilago suprascapularis, and it is anteriorly covered by the m. trapezius.

The m. *deltoideus scapularis* or m. dorsalis scapulae is a relatively long, well-developed muscle bordering anteriorly on the m. suprascapularis; it covers the m. serratus anterior and the origo of the m. serratus anterior superficialis. The origo on the outer surface of the cartilago suprascapularis lies postero-ventral to the insertio of the m. trapezius and extends ventrally far down on the lateral and posterior surfaces of the scapula. It runs external to the scapular heads of the m. triceps to its insertion on the central part of the pr. lateralis humeri. The insertio lies lateral to the lateral humeral head of the m. triceps and dorsal to the insertiones of the m. pectoralis and m. deltoideus inferior. The muscle covers the ventral part of the m. scapulo-humeralis anterior and the proximal parts of the scapular heads of the m. triceps. At its origo it is covered by the m. deltoideus inferior.

The m. deltoideus clavicularis of *Lacerta* is called the m. deltoideus coraco-sternalis s. inferior by Fürbringer (1900) since, with the loss of the clavícula, it has divided into two separate bellies. The dorsal belly or m.

coraco-humeralis anterior arises from the coracoid, and the ventral belly, or *m. sterno-humeralis anterior*, from the sternum. In *Microsaura* the *m. coraco-humeralis anterior* is a thin, broad muscle arising from the prominentia coraco-scapularis and adjoining anterior edge of the coracoid immediately anterior to the origo of the *m. supracoracoideus*. The *m. sterno-humeralis anterior* arises from the outer rim of the anterior part of the labium externum sulci coracoidei, but a few muscle fibres arise from the ventral attachment of the sterno-coracoid ligament which has replaced the clavícula; it persists in the adult. The insertiones of the two bellies on the pr. lateralis humeri are separate: the dorsal belly inserts distal to the insertio of the *m. deltoides scapularis* between the *m. coraco-brachialis brevis* and the origo of the lateral humeral head of the *m. triceps*. The ventral belly inserts proximal to the insertio of the *m. deltoides scapularis* and distal to the insertio of the *m. supracoracoideus*.

The *m. scapulo-humeralis anterior* is a small muscle with a tendinous origo on the outer rim of the scapular portion of the fossa glenoidalis. Where the tendon passes over the shoulder joint it is continuous with the shoulder capsule. The muscle is situated internal to the humeral ligament of the deep scapular head of the *m. triceps* and the insertio of the *m. deltoides scapularis*. The insertio is situated between the two humeral heads of the *m. triceps*.

The *m. subcoraco-scapularis* (subcoracoideus) and the *m. scapulo-humeralis posterior* (subscapularis) are found on the inner surface of the girdle. On account of their common origo on the pr. medialis humeri, Fürbringer (1900) calls these muscles collectively the *m. subcoracoscapularis*. In *Chamaeleo* the ventral belly or *m. subcoracoideus* originates from the coracoid only, but in *Microsaura* the *m. subcoraco-scapularis* originates not only from the inner surface of the coracoid (with the exception of the central part) but from the adjoining ventral part of the scapula as well. The muscle fibres converge to a tendinous insertio on the pr. medialis humeri. The *m. scapulo-humeralis posterior* is a relatively well-developed muscle with origo on the inner surface of the scapula dorsal to the attachment of the ligamentum sterno-scapulare internum. The tendinous insertio lies dorsal to that of the *m. subcoraco-scapularis* on the pr. medialis humeri, and is quite distinct.

The *m. triceps* (anconaeus) is a well-developed muscle with three origines on the shoulder-girdle: a scapular head (caput scapulare laterale *m. anconaei*), a lateral humeral head (caput humerale laterale *m. anconaei*) and a medial humeral head (caput humerale mediale *m. anconaei*). The scapular head has a double tendinous origo on the scapula: the larger superficial scapular head arises mainly as a tendon from the posterior surface of the scapula, well above the fossa glenoidalis. The smaller, deep scapular head arises as a tendon from the postero-ventral part of the scapula immediately dorsal to the fossa glenoidalis. It is "anchored" to the humerus by means of a ligament lying lateral to the *m. scapulo-humeralis anterior*. The lateral humeral head arises postero-medial to the insertio of the *m. deltoides scapularis*. The origo of the medial humeral head is situated medial to the insertio of the *m. scapulo-humeralis anterior*. The two humeral heads unite before they join the scapular head to form the *m. triceps* on the dorsal surface of the humerus. The insertio takes place on the ulna.

PART II

I RÉSUMÉ AND DISCUSSION

Scapulocoracoid

In the youngest stage the scapulocoracoid consists of actively condensing blastematous tissue the ventral part of which already encloses the n. supracoracoideus. The humerus, of course, develops in continuity with the scapulocoracoid and is a mass of dense blastematous tissue projecting into the limb bud. Chondrification of the pars scapularis commences in the region of the fossa glenoidalis, and in the 16.2 mm. stage its ventral part is chondrified. Perichondral ossification commences in the 18.8 mm. stage, and in the 19.5 mm. stage the shaft of the cartilago scapularis consists of highly hypertrophied chondrocytes ensheathed in a layer of perichondral bone. Endochondral ossification sets in at the 20.2 mm. stage. In the first stages the shaft of the cartilago scapularis gradually lengthens so that its dorsal end, or pars suprascapularis, already covers the upper parts of the two cervical and the first sternal rib in the 21.3 mm. stage. In this stage the scapula s. str. is well ossified and possesses a large single marrow cavity; perichondral ossification of the pars suprascapularis commences in the part adjoining the scapula.

The cartilago suprascapularis is not a separate element but is merely the unossified dorsal part of the pars scapularis of the embryo. The scapula s. lat. of *Microsaura* does not differ markedly from that of *Brookesia* (Siebenrock, 1893) and *Chamaeleo* (Parker, 1868; Fürbringer, 1876 and 1900) except that the cartilago suprascapularis of *Microsaura* is entirely covered by a thin layer of perichondral bone.

Chondrification of the planum coracoideum commences in the part adjoining the pars scapularis in the region of the fossa glenoidalis in the 16.2 mm. stage, and is continued in the next two stages. In spite of the advanced degree of chondrification in the 18.8 mm. stage, the two cartilagine coracoideae are still widely separated ventrally. In the 20.2 mm. stage the body of the cartilago coracoidea consists of highly hypertrophied chondrocytes and possesses a well-defined perichondrium in which the first signs of perichondral ossification appear. Its fringes still consist of procartilage. The cartilagine coracoideae overlap ventrally in the 21.3 mm. stage and have the adult appearance although there is no sign of endochondral ossification, such ossification commencing in the 21.9 mm. stage and continuing in post-natal life.

Overlapping of the coracoids has received much attention from workers on the *Anura* and has been called "arcifery"; but it is interesting that such overlapping is not confined to *Amphibia* but seems to be quite common in the *Lacertilia*. It has been observed in various forms such as *Lacerta* (Juhn, 1923; Van Gelderen, 1924-25), *Gongylus ocellatus* and *Ptychozoon homalocephalum* (Van Gelderen, 1924-25).

The coracoid in the adult is an unfenestrated, bony plate fringed with cartilage along its anterior, ventral and posterior borders. The only perforation is the foramen for the n. supracoracoideus. Parker (1868) calls the anterior and ventral borders the "prae-coracoid" and "epi-coracoid" respectively. Ac-

cording to Siebenrock (1893) *Brookesia* lacks an "epi-coracoid", and Fürbringer (1900) calls the coracoid of *Chamaeleo* a "Coracoid s. str." lacking procoracoidal elements. For reasons which will be explained below, these names are incorrect and misleading and have no morphological significance.

Much confusion has arisen about the nomenclature of the different elements comprising the ventral part of the tetrapod shoulder-girdle and their homologies. The term epicoracoid was first applied to the anterior coracoidal element in monotremes, and precoracoid (procoracoid) to the anterior element in amphibians and primitive reptiles. These terms were differently interpreted by various workers and have led to much confusion. It is impossible to review all the arguments that have been advanced, but a brief description of the most important works is perhaps desirable.

Parker (1868) described the shoulder-girdles of some lacertilian genera; he called the inferior cartilaginous border of the coracoid the "epi-coracoid" and a portion of the anterior cartilaginous expansion the "prae-coracoid". He regarded the single coracoidal element in living reptiles and birds as homologous with the coracoid of higher mammals, but he did not consider the anterior coracoidal element of monotremes as homologous with the amphibian procoracoidal cartilage.

Howes (1887 and 1893) pointed out that the mammalian coracoidal process is made up of two elements; the one which forms part of the glenoid cavity he regarded as homologous with the posterior element of the monotremes, and the rest of the pr. coracoideus as homologous with the anterior element in monotremes. Both elements in the monotreme coracoid he believed to correspond to the unpaired structure in birds and living reptiles. He called the anterior element in monotremes the epicoracoid and the posterior element the metacoracoid.

Broom (1899) showed that the coracoidal process of monotremes has a single centre of ossification and that one of the coracoidal processes in mammals is an epiphysis. He then believed that the two coracoidal processes of monotremes are homologous with the two found in fossil reptiles and with the two ventral elements in the shoulder-girdle of *Anura*. These are the procoracoidal cartilage and the posterior coracoid or the true coracoid; the former he believed to be lost in modern reptiles, birds and higher mammals and that the single ventral element was the true coracoid.

Bütschli (1910) considers the procoracoidal cartilage of *Urodela*, the clavicle plus the procoracoidal cartilage of *Anura*, the clavicle of the *Lacertilia* and the so-called procoracoid of *Chelonia* as homologous. He does not, however, consider the cartilaginous anterior part of the lacertilian coracoid as a procoracoid since this latter element invariably encloses a foramen for the n. supracoracoideus in the *Pelycosauria* (*Theromorpha*).

Fuchs (1912) studied the ontogeny of the clavicle in *Talpa europaea* and *Erinaceus europaeus*; he considers the cartilage occurring during the ontogeny of this structure as homologous with the procoracoidal cartilage of *Anura* and not as a neomorph. In 1927 Fuchs proposed the names taenia paracoracoidea medialis (s. posterior) for the "epi-coracoid" and taenia paracoracoidea anterior for the "prae-coracoid".

Most morphologists agree that there is a single coracoid in modern lizards, but there still seems to be disagreement as to which of the two

coracoidal elements of the early reptiles this single coracoidal element represents.

Williston (1911) described a single coracoid in *Varanosaurus* and in *Seymouria*, the most primitive reptile known. Broom (1912), Watson (1917) and Romer (1945) believe that in these forms the posterior element or true coracoid was absent or at least unossified. The procoracoid agrees with the single coracoid in modern reptiles in shape and in its perforation by a supra-coracoid foramen. Therefore, the single coracoid in modern lizards is the procoracoid. Broom (1912) demonstrates that the two coracoidal elements are retained through *Cotylosauria* to the mammal-like groups. The monotreme procoracoid is feebly developed, while in mammals only the posterior element or true coracoid is retained.

Gregory and Camp (1918) and Hanson (1920) on the other hand, believe that the posterior element had already been lost in *Varanosaurus* and therefore does not occur in living vertebrates. According to them the reptilian coracoid is a procoracoid and is homologous with the coracoid of mammals.

Howell (1936) considers the bony shoulder-girdle as a single element, the paraglenoid ossification; it expands in three directions: dorsal, cranial and ventral. Although these extensions of the paraglenoid ossification may be marked off by sutures, they are not separate elements. In *Eryops* the scapulo-coracoid is a continuous bone, but in the Lower Permian *Cotylosauria* the paraglenoid ossification is divided into scapular and coracoidal areas, marked off by a suture passing through the fossa glenoidalis. The cartilago supra-scapularis is merely an unossified portion of the dorsal expansion of the paraglenoid ossification. That part of the shoulder-girdle ventral to the fossa glenoidalis is associated with two distinct muscle groups: the anterior or coracohumeral and the posterior or coracobrachial group. Howell, therefore, concludes that the living lizard-like reptiles have posterior and anterior coracoidal areas, and not a single, undivided one as is generally believed.

In *Brookesia* (Siebenrock, 1893), *Chamaeleo* and *Uroplates* (Camp, 1923) and *Microsaura* the coracoid is an unfenestrated, bony plate fringed with cartilage, but in most lizards the coracoid is fenestrated or merely emarginated as in *Heloderma* (Camp, 1923). The first, and most lateral coracoidal fenestra ("primäres Fenster", Gegenbaur; upper coracoid fenestra, Parker) is frequently encountered, while the more medial fenestra ("sekundäres Fenster", Gegenbaur; lower coracoid fenestra, Parker; "Nebenfenster", Siebenrock) is of irregular occurrence. Most workers have adopted Parker's (1868) nomenclature, according to which the anterior cartilaginous border is the "prae-coracoid", the inferior cartilaginous margin the "epicoracoid" and that part behind the coracoid fenestrae the coracoid s. str.. When a second fenestra occurs, Parker calls the bar between the two fenestrae the "meso-coracoid". Various workers such as Götte (1877), Wiedersheim (1892) and Broom (1906) objected to this nomenclature since the coracoid develops from a single anlage.

The ontogeny of the shoulder-girdle of the *Lacertilia* has not received much attention, but in the few genera studied such as *Cnemidophorus* (Götte, 1877), *Lacerta agilis* (Wiedersheim, 1892), *Lacerta agilis*, *L. muralis* and *L. vivipara* (Bogoljubski, 1914), *Lacerta agilis*, *Gongylus ocellatus* and *Ptychozoon homalocephalum* (Van Gelderen, 1924-25), *Lacerta agilis*, *Mabuia* sp.

and some of the *Ascalabota* (Fuchs, 1927), the coracoid develops from a planar condensation of mesenchymatous tissue and has a single centre of ossification. Fenestration and emargination of the planum coracoideum occur very early during the ontogeny and results in the formation of the coracoidal fenestrae and of the incisura scapulo-coracoidea anteriorly. Complete resorption of the tissue does not occur so that the fenestrae, or "Reduktionsfenster" of Fuchs (1927), and emargination are closed by thin membranes, "Membrana obturatoria" of Fuchs (1927).

According to Gegenbaur (1865) and Fürbringer (1900) the ventral parts of the shoulder-girdle of the *Anura*, *Chelonia* and *Lacertilia* are homologous. Fuchs (1927) agrees with Götze (1877), Wiedersheim (1892), Bogoljubski (1914) and Van Gelderen (1924—25) that the ventral part of the scapulo-coracoid of *Lacertilia* is not homologous with that of the *Anura* and says: "Ontogenetisch gibt es also bei den Lacertiliern keinerlei Unterschiede zwischen den einzelnen Fenstern eines Schultergürtels: ontogenetisch gibt es kein Hauptfenster (Fenestra principalis) und keine Nebenfenster; ontogenetisch sind sie alle gleich und daher auch in gleicher Weise zu bewerten." (p. 338). In the *Anura* the fenestra situated between the coracoid, cartilago procoracoidea and pr. epicoracoideus is not the result of reduction, but is a primary fenestra, "Sprossungsfenster" of Fuchs (1926a).

The palaeontological as well as the ontogenetic evidence, therefore, seems to indicate that the coracoid of the living lizard-like reptiles is a single element and that the reptilian "prae-coracoid" and "epi-coracoid" have a purely topographic significance.

Clavicula and Interclavicula

The clavicula first appears in the 18.5 mm. stage in a patch of thickened blastematos tissue situated topographically ventro-medial to the anlage of the m. deltoides inferior and ventral to the anterior end of the cartilago coracoidea. Although the origin of this tissue is uncertain (stage IV), it does not develop in continuity with the scapulcoracoid. When concentration of the tissue in question first appears in an intermediate stage (17.8 mm.) it is quite discrete. The clavicula lengthens in a medio-ventral direction, and in the 18.8 mm. stage the tissue in which it is embedded is continuous with the undifferentiated perichondrium of the prominentia coraco-scapularis as well as with the ventral part of the m. deltoides inferior. In the 19.5 mm. stage the periosteum of the ventral end of the clavicula is in syndesmotomic continuity with the undifferentiated perichondrium of the anterior part of the labium externum sulci coracoidei. The clavicular vestige attains its maximum size at the 20.2 mm. stage and is 0.33 mm. in length. Resorption of the osseous tissue then commences, so that the bone appears in only two consecutive 10 μ sections in the 21.9 mm. stage. The former position of its dorsal and ventral ends is indicated by the sterno-coracoid ligament, running from the ventral part of the prominentia coraco-scapularis to the anterior part of the labium externum sulci coracoidei; it eventually replaces the clavicula completely and persists in the adult.

The anlage of the interclavicula appears in the 19.5 mm. stage and the bone itself in the 20.2 mm. stage only. It is formed by direct ossification of a

concentration of cells in the intersternal formative tissue in the region of the junction of the first pair of sternal ribs with the sternum. The origin of this intersternal formative tissue is uncertain. (stage VII).

The name clavícula was first applied to that part of the human clavícula which is not preformed in cartilage. The cartilage in connexion with its development was first discovered by Bruch (vide Nauck, 1938) and was confirmed by later workers such as Gegenbaur (1865) and Götte (1877) who regarded the clavícula of the *Anura* as a peripheral ossification of the procoracoidal cartilage. Braus (1909 and 1919) was the first to realise that the clavícula and the cleithrum of the *Anura* are membrane bones (*ossa investientia*). This was later confirmed by De Villiers (1922) and Fuchs (1922). Fuchs calls the clavícula the "os thoracale", since the clavícula of *Theria* is of composite origin; he regarded the pieces of cartilage occurring during the ontogeny of the bone as vestiges of the cartilago procoracoidea of lower forms. Such cartilage occurring during the ontogeny of the clavícula has led to much controversy among morphologists: Hanson (1920), Watson (1917), Hommes (1924) and others believe it to be neomorphic cartilage, while Fuchs (1912, 1922 and 1924), Zumpe (1925) and Nauck (1938) regard it as a procoracoidal vestige. A discussion of the arguments advanced does not seem profitable for the purpose of the present investigation, and the reader is referred to the works of the above-mentioned authors for detailed discussions of the problem.

The clavícula of the *Lacertilia* is, of course, never preformed in cartilage, but develops as a typical membrane bone although Camp (1923) claims that in some forms the clavícula may become cartilaginous in the final stages of reduction. Götte (1877) describes the ossification of the clavícula as similar to the ossification of a typical ossifying bar of cartilage so that the bone in question does not have its own marrow cavity. The anlage of the clavícula is supposed to be an outgrowth of the blastematos anlage of the primary shoulder-girdle (scapulocoracoid) in *Cnemidophorus* (Götte, 1877). The interclavícula ("episternum") has a paired origin, developing from caudally directed processes of the ventral ends of the clavícula. According to Gegenbaur (1865) the connexion between the clavícula and the scapulocoracoid is secondary: the clavícula resulting from direct ossification of a concentration of undifferentiated cells. Wiedersheim (1892) describes the clavicular anlage of *Lacerta agilis* as blastematos tissue derived from the scapulocoracoid, but in the seventh edition of his "Vergleichende Anatomie der Wirbeltiere" says: "Beziehung des Prokorakoids zur Clavikula treten nur noch in Spuren auf; die Clavikula entsteht vielmehr in ihrer grössten Ausdehnung isoliert, d.h. entfernt vom Prokorakoid, aus einem bindegewebigen Blastem." (1909, 187). Wiedersheim does not, however, motivate this statement. Bogoljubski (1914, 657) describes the anlage of the clavícula as follows: "Der Schultergürtel jeder Seite bildet in den Frühen Stadien der embryonal-bindegeweblichen Anlage ein einheitliches Blatt für die Pars scapularis, P. coracoidea und teils P. claviculäris." The clavícula and interclavícula develop from the same concentration of embryonic connective tissue, but he could not demonstrate any direct continuity between these two bones. According to Van Gelderen (1924-25) the clavícula and interclavícula are separate ossifications of a patch of blastematos tissue derived from the scapulocoracoid (sic.). Incomplete resorption of the tissue in question later results in the formation

of the membrana episterno-clavicularis. Neither Bogoljubski nor Van Gelderen could find any indication of an ossifactory process similar to that described by Götte (1877); according to these two workers the marrow cavity of the clavícula develops later during the ontogeny, which is, of course, not surprising. Fuchs (1927) agrees with Gegenbaur (1865) that the clavícula is a membrane bone in spite of the circumstances that its anlage develops in continuity with the scapulocoracoid.

The earliest anlagen of the clavicular and interclavicular vestiges of *Microsaura* do not develop in continuity with the scapulocoracoid or with each other, but occur in two separate condensations of embryonic tissue of uncertain origin. During its brief existence the clavícula remains solid without any indication of a marrow cavity.

Siebenrock (1893) considers the sterno-coracoid ligament of *Brookesia* and *Chamæleo* as homologous with the clavícula. Fürbringer (1900) raised objections to this, since the adult animal lacks an acromion as well as a clavícula, and specially because the ligament occupies a more ventral position than the clavícula does in other *Lacertilia*. He calls the anterior protuberance of the scapulocoracoid a prominentia coraco-scapularis, since the adult lacks a clavícula and the protuberance consists partly of scapula and partly of coracoid and could therefore not be regarded as homologous with the acromion of other *Lacertilia*. Broom (1906) describes a clavícula in an embryo of *Chamæleo* and also some indication of an acromial process in the lower part of the scapula, projecting a little further forward than the coracoid.

During the ontogeny of the shoulder-girdle of *Microsaura* a clavícula does occur; it is suspended between the prominentia coraco-scapularis and the anterior part of the labium externum sulci coracoidei by means of connective tissue. Later during the ontogeny resorption of the osseous tissue of the clavicular vestige takes place, the former position of the clavícula being indicated by the sterno-coracoid ligament. Although this ligament occupies a more ventral position in the adult animal, it functionally supplants the clavícula of other *Lacertilia*. The occurrence of a clavícula during the ontogeny in *Microsaura* proves that the prominentia coraco-scapularis is an acromial process. The presence of an acromion does not necessarily imply the occurrence of a clavícula; in many of the *Anura* the dorsal end of the clavícula does not articulate with the acromion at all (Nauck, 1938).

Sternum

Before discussing the sternogenesis in *Microsaura*, it may be useful to preface the description of this structure with a short general discussion.

The sternum is a cartilaginous or bony structure occupying a medio-ventral position in the anterior part of the trunk in *Vertebrata*. No agreement has yet been reached concerning its origin and homology and the designation is therefore used in a purely descriptive (topographical) sense. The classical theory on the origin of the sternum is Ruge's (1880) costal theory which derives the sternal anlagen from the ventral ends of the ribs ("Costosternum" of Fuchs, 1930). This theory based on human embryology, is in accordance with the work of Götte (1875) on *Anura* and *Salamandra* and is confirmed by the works of Schauinsland (1900 and 1906) on *Sphenodon*, C. Müller (1906)

on man, O. Müller (1913) on *Anguis*, Krieg (1919) and Juhn (1923) on *Lacerta*, Knopfli (1918) on *Aves* and Engler (1929) on *Urodela*. A second theory postulates that the sternal anlagen arise in continuity with the anlagen of the shoulder-girdle ("Zonosternum" of Fuchs, 1930), especially the coracoidal anlagen; this theory is supported by the works of Götte (1875) on *Ramidae*, *Chamaeleontidae* and *Crocodylia*, Paterson (1904) on mammals and Kälin (1929) on *Crocodylia*, especially *Alligator mississippiensis*. A third theory derives the sternum from two autochthonous longitudinal anlagen situated in the lateral body-wall or from a single medio-ventral anlage in the linea alba. This theory is at present regarded as the most probable, and is supported by the works of Kravetz (1905), Whitehead and Waddell (1911), Bogoljubski (1914), Hanson (1920), Van Gelderen (1922 and 1924-25), Hommes (1925) and Gladstone and Wakeley (1932).

In some *Anura*, however, the sternum has been proved to have a mixed origin: the anterior part is zonal and the posterior part arises as autochthonous anlagen. In *Bombina* and *Alytes* the sternum is partly of zonal and partly of inscriptional origin (De Villiers, 1922), while Fuchs (1926b) derives the anterior part of the sternum in *Anura* from the girdle. The circumstance that the sternum in *Amphibia* has a non-costal origin, prompted Howes (1891) to call it an "archisternum", and the sternum of *Amniota* a "neosternum". On account of its mixed origin, Fuchs (1922) named the anterior part of the anuran sternum the "Praezonale" and the posterior part the "Postzonale". De Villiers (1922) maintains that in those groups in which the sternum does not have a costal origin, there is no justification for calling it a sternum at all, but retains the term in subsequent papers, for historical reasons.

The sternum is lacking in *Chelonina*, *Ophidia* and certain limbless *Lacertilia*. In *Rhynchocephalia* the sternum is a single, broad, fenestrated plate of cartilage resembling the praesternum of *Crocodylia* and *Lacertilia*. In these two orders the sternum generally consists of a broad, anterior part or praesternum and a slender posterior part or meso-xiphisternum. The names prae-, meso- and xiphisternum were proposed by Parker (1868) and are now generally accepted, although they have no morphological significance. In most lizards the praesternum is fenestrated, having one or two windows to which Camp (1923) assigns a certain systematic value. Siebenrock (1895) regards them as primary fenestrae, but according to Bogoljubski (1914) the fenestra in *Lacerta* develops secondarily by resorption of the sternal tissue after complete fusion of the two halves of the sternum has taken place. As a rule the sternum of *Reptilia* is "unsegmented", but Parker (1868) and Gegenbaur (1898) describe a "segmented" sternum in *Chamaeleo* and *Anguis* regarding this feature as a specialization.

Rathke (1853 and 1862) considered the reptilian sternum as non-costal in origin; it consists of an anterior bony element (the interclavicula, a membrane bone) and a larger, posterior cartilaginous element (true sternum). In "typical" *Lacertilia*, with the exception of the *Chamaeleontidae* in which an interclavicula is absent, this anterior element usually consists of a central stem with two lateral prolongations. Rathke distinguishes an anterior and a posterior portion in the single, cartilaginous posterior element.

Parker (1868) named the anterior part of the sternum the praesternum and the posterior part the meso-xiphisternum, the "xiphisternum" being that

part which is continued behind the junction of the last pair of sternal ribs. He also considered the sternum of all *Vertebrata* as arising from the lower parts of some of the costal arches.

Götte (1877) described an embryo of *Cnemidophorus* in which the first sternal rib is continuous with the sternal anlage, the last two cervical ribs being connected to this latter element by means of dense mesenchymatous tissue. Götte believed that the primary connexion between the sternal anlage and the last two cervical ribs had already been lost. In an older embryo three sternal ribs are continuous with the sternal anlage. Götte, therefore, believed that the sternal anlage originate from the ventral parts of the last two cervical and the first sternal rib, and that the last two sternal ribs contribute to the formation of the posterior part of the sternum.

Wiedersheim (1892) came to the same general conclusions as Götte (1877) and derives the sternum of *Lacerta agilis* from the ventral ends of four pairs of ribs, the last cervical rib probably also taking part in the formation of the sternum. He regarded the tissue from which the autotochthonous anlagen of the sternum of *Anura* and *Urodela* develop as derivatives of the myocommata giving rise (?) to the ribs, and therefore considered their sterna of costal origin.

Gegenbaur (1898) regards the sterna of the different groups of *Amniota* as homologous structures developing from the ventral ends of the ribs. Fürbringer (1900) also supports Ruge's (1880) costal theory and agrees with Gegenbaur (1898) that the posterior part of the sternum (meso-xiphisternum, Parker; metasternum, Gegenbaur) is the most recently acquired part of the sternum, and is still in "statu nascendi".

Bogoljubski (1914) working on embryos of *Lacerta agilis*, *L. muralis* and *L. vivipara*, maintains that the sternum arises as two discrete, triangular, mesenchymatous anlagen; these structures are at first situated in the lateral body-wall, posterior to the coracoids and ventral to the ends of the ribs and appear later than the coracoidal anlagen. Fusion of the ribs with the sternal plates takes place in serial order, commencing with the first. Only after the fifth pair of sternal ribs has joined the sternal plates, do these latter structures fuse. Fusion of the anterior and posterior ends of the sternal plates takes place simultaneously to form a single, solid cartilaginous sternum. The fenestra sterni is formed later in the ontogeny by resorption of the sternal tissue. In *Anguis fragilis* the sternum arises in the same way. Bogoljubski concludes that the origin of the sternum is in the linea alba, and homologises the sternum (including the xiphisternum) of *Mammalia* with the entire sternum of *Reptilia*.

Van Gelderen (1922a), working on embryos of *Lacerta agilis*, *Gongylus ocellatus* and *Ptychozoon homalocephalum*, came to the same general conclusions as Bogoljubski (1914). In the three genera investigated, the sternum has a paired anlage consisting of dense blastematous tissue; such anlagen are situated in the lateral body-wall, and have no primary connexion with either the ribs or the coracoidal anlagen. In *Lacerta agilis* three pairs of sternal ribs fuse with the sternal anlagen; the fourth pair joins a caudally directed process of the sternal plate, and the fifth pair joins this latter pair well behind the junctional region. When the two sternal plates eventually fuse, the ventral ends of the fifth and fourth pairs of sternal ribs form the "xiphisternum", which may be compared with Wellborn's (1933) "Ventrocostalsternum". On

account of the autochthonous origin of the sternum in *Amphibia* and the praesternum in *Amniota*, Van Gelderen (1922b, 2235) considers these structures as homologous and calls the praesternum an "autochthone borstbeen" and the xiphisternum of *Amniota* a "costale borstbeen dat onto-, en phylogenetisch jonger is".

Juhn (1923) criticizes Bogoljubski (1914) and Van Gelderen (1922a), basing her arguments on embryos of *Lacerta agilis*, *L. vivipara* and *L. muralis* which she believed to be younger than theirs. When the sternal anlagen appear the ventral ends of the sternal ribs are in continuity with them, thus confirming Ruge's costal theory.

In *Microsaura* the earliest anlagen of the sternum appear in the 13.9 mm. stage as two discrete, longitudinal condensations of blastematos tissue in the lateral body-wall. They are situated medio-ventral to the apices of the anlagen of the intercostal musculature and posterior to the plana coracoidea. The anlagen are separated from these latter structures by means of loose embryonic connective tissue and are continued up to a point immediately behind the blastematos tip of the third thoracic rib. During the two following stages the anterior ends of the sternal anlagen lengthen, so that they lie medio-ventral to the ventral borders of the plana coracoidea. Progressive downgrowth of these latter structures results in condensation of the embryonic connective tissue lying between the anterior ends of the sternal anlagen and the ventral procartilaginous borders of the plana coracoidea. In the 18.5 mm. stage, therefore, the anterior ends of the sternal anlagen appear to be continuous with the cartilagine coracoideae, but in sections stained in Bismarck-brown (a stain specific for cartilage matrix) the true nature of this tissue becomes apparent: it fails to take up the stain. In the 18.8 mm. stage the anterior ends of the two halves of the sternum have broadened considerably as a result of deposition of intercellular matrix in the blastematos tissue situated medial to their ventral ends, and in the blastematos tissue situated between the posterior end of the cartilago coracoidea and the anlage of the pars sternalis musculi pectoralis. This latter tissue which is continuous with the undifferentiated perichondrium of the anterior end of the sternum, is the anlage of the labium externum sulci coracoidei. The labium internum develops in the same way as the labium externum: by means of deposition of intercellular matrix in the blastematos tissue situated between the postero-medial border of the cartilago coracoidea and the anlage of the m. sterno-costo-coracoideus. In the 19.5 mm. stage the apparent continuity between the sternal anlage and the cartilago coracoidea is lost when resorption of the dense embryonic connective tissue situated between the anterior end of the sternal anlage and the cartilago coracoidea marks the initiation of a synovial cavity between these two structures.

Fusion of the sternal ribs with the sternum is secondary and takes place in serial order, commencing with the first. In the procartilaginous condition of the ribs and the sternum the ventral ends of the ribs are connected with the sternum by means of dense blastematos tissue in which intercellular matrix is subsequently deposited. There is therefore no histogenetic evidence whatsoever of the sternum arising from the ribs: they chondrify separately. Each half of the sternum is continued behind the junction of the third sternal rib as a so-called "xiphisternal" process which develops as part of the sternum and has no connexion with the ribs.

Fusion of the two halves of the sternum only takes place after the ribs have fused with it. During ontogeny the two halves of the sternum gradually approach each other ventrally so that fusion of their anterior ends takes place in the 20.2 mm. stage. The two halves of the sternum do not fuse in an antero-caudal direction from this point; in the 21.9 mm. stage the anterior parts of the mesosternum in the region between the junctions of the first and second sternal ribs become contiguous and eventually fuse. Fusion of the mesosternum proceeds anteriorly and posteriorly, starting from this region, and affects the posterior parts of the praesternum. Complete fusion of the two halves of the praesternum does not take place, consequently their inner edges remain separated and bound the fenestra sterni. Complete fusion of the two halves of the mesosternum results in the unpaired, dorso-ventrally flattened mesosternum of the adult animal; the xiphisternal processes fuse incompletely to form the fenestrated xiphisternum.

Perichondral ossification of the sternum commences at a time when its two halves are still separated, and is continued in post-natal life so that the entire sternum of the adult, with the exception of the outer edges of the labia sulci coracoidei and the mid-line, is ensheathed by a thin, discontinuous layer of perichondral bone.

The mesosternum of *Microsaura* does not develop as a caudally directed process of the praesternum: it represents the chondrified postero-medial part of the original, blastematous sternal anlagen, and is, therefore, not homologous with the xiphisternum of *Lacerta* which consists of the fused ventral parts of the fourth and fifth sternal ribs (Bogoljubski, 1914 and Van Gelderen, 1924-25). Also, the fenestra sterni of *Microsaura* is not formed by resorption of the sternal tissue as in *Lacerta* (Bogoljubski, 1914 and Juhn, 1923), but has resulted from the incomplete fusion of the two halves of the praesternum. The membrane closing it is formed by the intersternal tissue and, therefore, differs from that of *Lacerta* which is a "Reduktionsmembran" (Fuchs, 1927).

The sternum of *Microsaura* differs from that of *Brookesia* in being perichondrally ossified. Parker (1868) describes a similar ossification of the sternum of *Chamaeleo vulgaris* and *C. pumilus* (*Microsaura*), but Rathke (1852) did not notice it. According to Parker (1868) the ribs articulate with the sternum in *C. vulgaris* by means of synovial joints; but in the present investigation such synovial cavities were nowhere observed: the ribs are always sychondrotically connected with the sternum.

The fenestra sterni has never been mentioned by any worker on the *Chamaeleontidae*. Methuen and Hewitt (1913) described and figured the sterna of several species of *Chamaeleo* and *Brookesia* but did not mention nor figure this fenestra. In *Microsaura* the fenestra is small and closed by means of dense connective tissue so that it is very easily overlooked in dissection. It is, however, a constant feature of the sternum; its position varies individually but in adult specimens it is situated somewhat anteriorly in the praesternum.

The mesosternum is absent in *Brookesia*, and two pairs of sternal ribs join the praesternum. Siebenrock (1893) regards the ventral ends of the third pair of sternal ribs which fuse before they join the praesternum, as a "xiphisternum". The different species of *Chamaeleo* described by Methuen and Hewitt (1913), all possess a well-developed xiphisternum; the degree of development and shape of this structure varies considerably, and is very well developed in *Chamaeleo lateralis*.

Behind the xiphisternum the ventral ends of the fourth pair of thoracic ribs are synchondrotically connected; there is no connexion with the xiphisternum, nor is there any indication of a supplementary plate or "meta-sternum" such as was noted by Parker (1868) in *Chamaeleo vulgaris* and *C. pumilus* (*Microsaura*), and by Siebenrock (1893) in *Brookesia superciliaris*.

At present it is impossible to make a conclusive statement on the morphological relations of the sternum in *Lacertilia*, since the sternogenesis of only a few genera is known. A final statement can only be made after extensive research, with special attention to the histogenesis of the various parts of the sternum, has been carried out. As regards the praesternum, there seems to be a tendency to break away from Ruge's (1880) costal theory, although this theory cannot be disregarded, since it still applies to parts of the sternum. It seems, however, as if too much attention has been paid to the circumstance that the anlagen of the sternum develop in continuity with the ribs in some forms, while in others it develops from autotochthonous anlagen. These circumstances could possibly be regarded as a coenogenetic phenomenon, and, therefore, of secondary importance in morphology.

Post-sternal Ribs

Posterior to the sternum the ventral parts of eight pairs of ribs are, serially, synchondrotically connected to form eight costal hoops encircling the abdomen. These true ribs have erroneously been referred to as "abdominal ribs" or parasternalia (parasternum). These terms originally designated membrane bones situated in the ventral abdominal musculature of *Sphenodon* and *Crocodylia*, but have been applied by morphologists to skeletal elements in the abdominal musculature of *Amphibia* and other reptiles. Some of these elements are not of dermal origin, so that the terms have now acquired a double meaning. De Vos (1938) investigated the cartilaginous inscriptional ribs in *Leiopelma*, and the reader is referred to her work for a comprehensive review of the literature dealing with these structures in *Vertebrata*. The term "abdominal ribs" is misleading, since these structures are not ribs at all but modified vestiges of the ventral dermal armature of fishes, *Stegocephalia* and fossil reptiles. De Vos (1938) advocates the use of the term gastralialia, originally applied to the rib-like abdominal dermal bones in *Sphenodon* by Baur (vide De Vos, 1938).

Gastralia are found in *Sphenodon*, *Crocodylia* and many other reptiles. According to Voeltzkow and Döderlein (1901) who studied the ontogeny and morphogenesis of these structures, gastralialia are membrane bones originating in the cutis layer of the myotome and their pseudo-inscriptional position in the ventral abdominal musculature is quite secondary. Needless to say, inscriptional ribs frequently ossify. De Villiers (1926) maintains that the only valid criterion for distinguishing ossa investientia from ossa substituentia, as defined by Gaupp (1906), is the histogenetic one.

Musculature

The ontogeny of only two muscles was studied in detail, since they differ markedly from those of *Lacerta*, as described by Romer (1944). The other muscles of the breast-shoulder apparatus do not differ very much from those of *Lacerta* in the adult, and their ontogeny broadly corresponds to that in *Lacerta* except for minor details.

The m. supracoracoideus of *Lacerta* is a single muscle belonging to the ventral pectoral group (Romer, 1944). In the *Chamaeleontidae* it is represented by the m. supracoracoideus and the m. suprascapularis, which Fürbringer (1900) collectively calls the m. supracoracoscapularis on account of their common innervation by the n. supracoracoideus. The ontogeny of these two muscles in *Microsaura* proves Fürbringer's views to be correct. The anlagen of the muscles of the shoulder-girdle and of the humerus appear for the first time in the 13.9 mm. stage. The single anlage of the m. supracoracoscapularis covers the outer surface of the planum coracoideum and the ventral part of the cartilaginous pars scapularis. The dorsal part of this anlage increases in length together with the pars scapularis and becomes incompletely separated from the ventral part during subsequent stages; the insertio on the pr. lateralis humeri, however, remains single. In the adult animal the dorsal part of the m. suprascapularis has its origo on the antero-lateral surface of the scapula, but the ventral part, or m. supracoracoideus, has its origo on the anterior, outer surface of the coracoid immediately posterior to the origo of the m. coraco-humeralis anterior. The two bellies, however, have a common insertio on the pr. lateralis humeri and are innervated by the same nerve: the n. supracoracoideus.

The m. deltoideus clavicularis of *Lacerta* has apparently differentiated into two bellies: a dorsal, or m. coraco-humeralis anterior and a ventral, or m. sterno-humeralis anterior. It should actually be called a m. deltoideus coraco-sternalis s. inferior (Fürbringer, 1900). In *Microsaura* the m. deltoideus inferior has a single anlage situated dorso-lateral to the anlage of the clavícula. In the 19.5 mm. stage the anterior portion of this anlage has divided into two bellies. The dorsal belly, or m. coraco-humeralis anterior, arises from the anterior border and adjacent outer surface of the cartilago coracoidea as well as from connective tissue between the dorsal end of the clavícula and the prominentia coraco-scapularis. Part of the muscle, however, arises from the periosteum of the dorsal end of the clavícula itself. The ventral belly, or m. sterno-humeralis anterior, arises as a thin sheet of muscle along the posterior rim of the clavícula and the labium externum sulci coracoidei; the insertio on the pr. lateralis humeri, however, remains single. In the 20.2 mm. stage the origo of both bellies on the clavícula is practically lost. During subsequent stages the m. coraco-humeralis anterior gradually attains a larger origo on the coracoid, and the origo on the dorsal end of the sterno-coracoid ligament is diminished and eventually lost. In the adult animal the m. sterno-humeralis anterior arises mainly from the anterior part of the labium externum sulci coracoidei, but a few fibres arise from the ventral attachment of the sterno-coracoid ligament which has replaced the clavícula. The insertiones of the two bellies on the pr. lateralis humeri are separate in the adult animal.

II SUMMARY AND CONCLUSIONS

- 1 The shoulder-girdle of *Microsaura* does not resemble, very closely, that of the more typical *Lacertilia* or even that of the primitive chamaeleontid *Brookesia*, but is more like that of *Chamaeleo*.
- 2 The cartilago suprascapularis is entirely ensheathed by a thin layer of perichondral bone.

- 3 The whole of the scapula is ossified, such ossification having proceeded from a single centre.
- 4 The coracoidal plate is a single element developing from an unfenestrated anlage and has one centre of ossification only; it is not entirely ossified in the adult but is fringed with cartilage covered by a thin layer of perichondral bone. It is entirely without fenestrae and is pierced by a foramen through which the n. supracoracoideus passes.
- 5 The scapular and coracoidal regions are in synchondrotic continuity, and both of them bound the fossa glenoidalis.
- 6 At the border of the scapula and the coracoid each possesses an anterior, bony process: the two processes thus formed are covered with a continuous cartilage sheath and form the prominentia coraco-scapularis which is an acromial process.
- 7 A clavacula and interclavacula occur during ontogeny but have disappeared in the adult animal.
- 8 The clavacula is replaced by the sterno-coracoid ligament.
- 9 The sternum arises as two discrete, longitudinal condensations of blastematos tissue.
- 10 For a short time during ontogeny the anterior ends of the sternal anlagen apparently effect continuity with the cartilagine coracoideae.
- 11 Fusion of the two halves of the sternum takes place only after they have been joined by three pairs of sternal ribs; such fusion is incomplete. The inner edges of the praesternum remain separate and bound the fenestra sterni.
- 12 The sternum remains cartilaginous throughout life and is covered by a thin discontinuous layer of perichondral bone except along the edges of the praesternum and along the mid-line.
- 13 The praesternum is fenestrated and grooved along its antero-lateral borders for the reception of the coracoids. The first pair of sternal ribs is synchondrotically connected with the praesternum.
- 14 The intersternal tissue is skeletogenous and contributes to the formation of the praesternum.
- 15 The mesosternum represents the postero-medial part of the original sternal anlagen and is synchondrotically connected with the second and third pair of sternal ribs.
- 16 The xiphisternum is fenestrated and represents the incompletely fused xiphisternal processes of each sternal half; it is part of the original sternal anlagen and of non-costal origin.
- 17 The so-called "parasternalia" ("Ventricostalsternum") consist of the ventral ends of eight pairs of thoracic ribs which are, serially, in synchondrosis in the ventral mid-line.
- 18 In *Microsaura* the m. supracoracoideus of *Lacerta* is represented by the m. supracoracoscapularis, consisting of the m. supracoracoideus and the m. suprascapularis, both innervated by the n. supracoracoideus. In the adult these two muscles which have developed from the same anlage have a common insertio on the pr. lateralis humeri.
- 19 The m. deltoideus inferior (m.d. clavicularis of *Lacerta*) consists of two bellies: a dorsal, or m. coraco-humeralis anterior and a ventral, or m. sterno-humeralis anterior. The two bellies are completely separated in the adult animal, but originate from a single anlage.

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*Not seen in the original.

'N STUDIE VAN DIE LIGGAAMSBOU EN LIGGAAMSGROEI VAN BLANKE EN KLEURLINGSEUNS IN DIE WESTELIKE PROVINSIE, OUDERDOMSGROEP 13 TOT 17 JAAR

deur

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(Met 73 Tabelle en 25 Teksfigure)

Skripsie goedgekeur ter verkryging van die graad Magister in die
Natuurwetenskappe aan die Universiteit van Stellenbosch

Ingelewer: Februarie 1958

ABSTRACT

Anthropometric measurements of 474 European and 500 Cape Coloured boys, from 13 to 17 years, living in the Western Province, were made between 1955 and 1957. The average stature and weight have increased by 21.6 cm. and 54 lb. in the case of the European boys and 22.9 cm. and 43 lb. in the case of the Cape Coloured boys. The former are physically taller and the differences between the two groups are statistically significant. The Cape Coloured boys show a greater percentage increase in body length whereas the European boys show a greater percentage increase in breadth and circumference measurements.

In European boys the earlier termination of adolescent growth spurt and the earlier appearance of pubic hair leads to the conclusion that puberty starts slightly earlier. The statistical analysis proves that the Cape Coloured are as homogeneous a group as the European boys.

Bladsy

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I INLEIDING

Hierdie ondersoek is 'n bydrae tot ons kennis van die liggaamsgroei van die Suid-Afrikaanse blanke seuns in vergelyking met dié van Kleurlingseuns van dieselfde ouderdom. Dié tema het ek gekies op voorstel van Dr. C. S. Grobbelaar, nog voor sy aftrede in 1956 as senior lektor in Soölogie en Fisiese Anthropologie aan die Soölogiese Instituut, Universiteit van Stellenbosch.

Die eerste deel van hierdie beskrywing is 'n vergelyking van die toename in liggaamsgroei soos gesien in die berekende gemiddeldes van die absolute liggaamsmate. Die tweede deel is 'n vergelyking van sekere liggaamsverhoudinge of indekse van die twee groepe van dieselfde ouderdom, 13 tot 17 jaar. Die liggaamsmate is in die tydperk 1955—1957 geneem.

Die Kleurlinge is as 'n groep vir die eerste keer fisies-anthropologies ondersoek deur Van Wyk (1939). Sy resultate word later vergelyk met die bevindings i.v.m. die 17-jarige Kleurlingseuns. Keen (1949) het hom veral bepaal tot 'n kraniologiese studie van dieselfde bevolkingsgroep. Albei ondersoekers het hulle tot volwassenes bepaal. Hierdie ondersoek is van belang omdat dit 'n bydrae is tot 'n vergelyking van blanke en Kleurlingskoolseuns ten opsigte van liggaamsbou en liggaamsgroei soos gesien in die liggaamsmate van seuns van hul 13de jaar tot hul 17de jaar. Aangesien hierdie leeftye binne die puberteitsjare val, sal die gevolgtrekkings in die teken staan van die moontlike verskille wat daar optree, tussen blanke en Kleurlingseuns gedurende hierdie jare.

II MATERIAAL

Die materiaal het bestaan uit die blanke en Kleurlingseuns in die skole in die Westelike Provinsie onder die Departement van Openbare Onderwys van die Kaapprovinsie. Volgens Cruse (1947) wys die benaming Kaapse Kleurling daarop dat die Kleurlinge in die Kaapkolonie, meer bepaald in die Westelike Provinsie ontstaan het en hulle tuiste daar gevind het. Hierdie bevolkingsgroep se ontstaan as 'n aparte eenheid is die gevolg van ontstamming, aanvaarding van die blanke bevolking se kultuur en taal, en bloedvermenging (hetsy tussen nie-blanke rasse onderling en/of tussen blankes en nie-blanke).

Altesaam 474 blanke en 500 Kleurlingseuns is gemeet.

Die verspreiding van die twee groepe en die getalle in die betreffende skole gemeet, word in Tabele 1 en 2 aangegee.

Die betrokke blanke en Kleurlingseuns soos aangegee in tabel 1 en 2, is almal gebore of woonagtig vir die afgelope 5 jaar in die Westelike Provinsie in die gemelde dorpe.

III METODE EN TEGNIEK

Al die mate is gestandaardiseer: d.w.s. hulle is liggaamsmate waarvan die betekenis deur internasionale ooreenkoms vasgestel en omskryf word in Martin (1928) e.a.

Die meetpunte is bepaal, en die tegniese hantering van die meetapparate (instrumentarium) was volgens die voorskrifte van Martin (1928), Schlagin-

Tabel 1
Blanke seuns

Lokalteit	Aantal
Stellenbosch	124
Kaapstad	71
Paarl	64
Robertson	57
Strand	51
Somerset-Wes	26
Hermanus	25
Worcester	21
Tulbagh	13
+ Ander skole	42
	<hr/> 474

Tabel 2
Kleurlingseuns

Lokalteit	Aantal
Stellenbosch	148
Somerset-Wes	79
Kaapstad	68
Paarl	50
Strand	48
Wellington	36
Worcester	30
Kuilsrivier	19
Franschhoek	13
Caledon	9
	<hr/> 500

haufen (1946), en Bach (1930). Die volgende meetapparate is gebruik: antropometer, skuifpasser, krompasser, maatband en weegskaal. Die mate word in sentimeter aangegee en die gewig in ponde.

Die verskillende mate is op meegaande ondersoekvorm genoteer. (Sien bladsy 141.) Hulle is oorheersend in die namiddag van 2.30 nm.—4.00 nm. geneem om die daaglikse skommeling in die liggaamslengte uit te skakel.

Die proefpersoon was in 'n kortbroekie geklee, en die mate is op die ontblote liggaam geneem.

OUDERDOMSGROEPE

Die seuns is in ouderdomsgroepe volgens die metode van R. Martin (1928) geklassifiseer.

13 jaar = 12 jaar 6 maande — 13 jaar 5 maande
 14 jaar = 13 jaar 6 maande — 14 jaar 5 maande
 15 jaar = 14 jaar 6 maande — 15 jaar 5 maande
 16 jaar = 15 jaar 6 maande — 16 jaar 5 maande
 17 jaar = 16 jaar 6 maande — 17 jaar 5 maande

GEMIDDELDE OUDERDOM

Die gemiddelde ouderdom van die aantal seuns in elke ouderdomsgroep is bereken tot die naaste jaar en maand.

Tabel 3

Ouderdomsgroep	Gemiddelde ouderdom	
	Blanke	Kleurling
13	13 jaar 0 maande	13 jaar 0 maande
14	14 jaar 0 maande	13 jaar 10 maande
15	15 jaar 0 maande	15 jaar 0 maande
16	15 jaar 11 maande	16 jaar 0 maande
17	17 jaar 0 maande	16 jaar 10 maande

Tabel 4

Aantal seuns gemeet in elke ouderdomsgroep.

Ouderdomsgroep	Blanke	Kleurling
13	74	100
14	100	100
15	100	100
16	100	100
17	100	100

DIE ABSOLUTE MATE EN INDEKSE

Absolute mate:

Van elke individu (seun) is 2 kopmate en 27 liggaamsmate gemeet. (Die nommers teenoor elke maat verwys na die nommers waaronder die betreffende mate beskryf word in Martin (1928)):

1. Liggaamslengte
4. Hoogte van die suprasternale
5. Hoogte van die nawel
6. Hoogte van die symhysion
13. Hoogte van die regter-iliospinale
8. Hoogte van die regter-akromion (skouerhoogte)
23. Sithoogte

27. Lengte van die romp (van voor gesien)
17. Spanwydte van die arms
- 45 a. Lengte van die regterarm
- 53 (1). Lengte van die regterbeen
35. Skouerbreedte (afstand tussen akromia)
38. Mammillare breedte
40. Grootste bekkenbreedte
41. Iliospinale breedte
61. Borsomvang met normale, rustige respirasie
- 61 a. Borsomvang na diep inspirasie
- 61 b. Borsomvang na maksimale ekspirasie
36. Borsbreedte (transversale deursnee)
37. Borsdiepte (sagittale deursnee)
65. Grootste omvang van die regterbo-arm — gestrek
- 65 (1). Grootste omvang van die regterbo-arm — gespan
66. Grootste omvang van die regtervoorarm
68. Grootste omvang van die regterdy
69. Grootste omvang van die regterkuit
- 62 (1). Buikomvang (op die hoogte van die nawel)
71. Gewig.

Kopmate:

1. Grootste lengte van die kop
2. Grootste breedte van die kop.

Indekse:

Gebruikmakende van die berekende gemiddelde mate, is vir elke ouderdomsgroep 22 indekse (liggaamsverhoudinge), bereken.

Liggaamsmate relatief tot liggaamslengte:

Relatiewe hoogte van die suprasternale
 Relatiewe hoogte van die nawel
 Relatiewe hoogte van die symphysis
 Relatiewe hoogte van die iliospinale
 Relatiewe voorste romplengte
 Relatiewe sithoogte
 Relatiewe spanwydte
 Relatiewe beenlengte
 Relatiewe armlengte
 Relatiewe buikomvang

Liggaamsmate relatief tot romplengte:

Relatiewe armlengte
 Relatiewe beenlengte
 Relatiewe mammillare breedte
 Relatiewe iliospinale breedte
 Relatiewe bekkenbreedte

Ander indekse bereken:

Armlengte relatief tot beenlengte (intermembrale indeks)
 Iliospinale breedte relatief tot bekkenbreedte

Bekkenbreedte relatief tot skouerbreedte
 Voorarmomvang relatief tot bo-armomvang
 Kuitomvang relatief tot borsbreedte
 Kopbreedte relatief tot koplengte.

STATISTIESE ANALISE VAN DIE LIGGAAMSMATE

By elke reeks absolute mate is die volgende berekenings en die maksimale en minimale mate aangegee.

- 1 *Rekenkundige gemiddelde* (M)
- 2 *Standaardafwyking* (s): Die standaard-afwyking is 'n maatstaf wat die graad van verspreiding van die individuele mate om die gemiddelde aandui.
- 3 *Standaardfout van die gemiddelde* ($\pm m$): Die waarde hiervan dui aan hoe naby die berekende rekenkundige gemiddelde by die teoreties werklike gemiddelde kom.
- 4 *Variasiekoëffisiënt* (v): Waar die standaardafwyking(s) die verspreiding van die variasie om die rekenkundige gemiddelde aandui, stel die variasie-koëffisiënt 'n persentuele variasie voor. Dit stel ons dus in staat om die graad van variasie wat tussen twee reekse voorkom, met mekaar te vergelyk; bv.:

Die gemiddelde iliospinale breedte van blanke seuns, in die ouderdoms-groep 16 jaar, is 22.0 sm. met $s = 1.78$ sm., en in die geval van kleurlingseuns is die gemiddelde 19.9 sm. met $s. = 1.76$ sm. Hieruit is dit duidelik dat die iliospinale breedte by die blanke seuns groter is. Om die variasies, soos dit by die twee groepe voorkom, met mekaar te vergelyk, moet die persentuele variasie of variasiekoëffisiënt bereken word.

$$\text{Blanke:} \quad v = \frac{1.78 \times 100}{22.0} = 8.09\%$$

$$\text{Kleurling} \quad v = \frac{1.76 \times 100}{19.9} = 8.79\%$$

Die gevolgtrekking is dus dat alhoewel die absolute variasie by die blanke seuns groter is, die graad van variasie by die Kleurlinge, uitgedruk as 'n persentasie van die gemiddelde, effens groter is.

5 *Die t-toets vir betekenis van verskille tussen rekenkundige gemiddeldes:*

Omdat daar deurgaans verskille tussen die rekenkundige gemiddeldes van die mate vir blanke en Kleurlingseuns voorkom, was dit uiters belangrik om te toets of die verskille werklike of toevallige verskille is.

Formule vir t-toets:

$$t = \frac{\frac{\bar{M}_B - \bar{M}_K}{\sqrt{\frac{1}{N_B} + \frac{1}{N_K}}}}{S}$$

- \overline{M} = Rek. gem.
 B = Blanke
 K = Kleurling
 V = Vryheidsgrade
 S = 'n Beraming van standaardafwyking en waar t gebaseer is op

$$V = N + N - 2.$$
 B K
 In gevalle waar variasies betekenisvol verskil,
 is 'n noukeurige t-toets toegepas.

VOLGORDE WAARIN DIE MATE GENEEM IS

By elke seun, met die uitsondering van 'n paar waar net liggaamslengte en gewig gemeet is, is 'n volledige stel mate geneem. Die hulp van 'n assistent was altoos nodig om die mate, gedurende die meting, in die ondersoekvorm wat vir dié doel ontwerp is, af te skrywe.

- 1 Nadat die nodige meetpunte gepalpeer is, is met die antropometer die volgende lengteas-mate van die model in die gestandaardiseerde staanposisie gemeet:
 - Liggaamslengte
 - Hoogte van die suprasternale
 - Hoogte van die nawel
 - Hoogte van die symphysis
 - Hoogte van die regter-iliospinale
 - Hoogte van die regter-akromion
 - Hoogte van die regter-daktylion
- 2 Met die arms horisontaal gestrek is die spanwydte van die arms gemeet.
- 3 Met die model in die gestandaardiseerde sitposisie is die sithoogte gemeet.
- 4 Die volgende breedtemate is hierna in die staanposisie gemeet:
 - Skouerbreedte
 - Mammillare breedte
 - Grootste bekkenbreedte
 - Iliospinale breedte
- 5 Daarna is die volgende borsmate met die bandmaat gemeet:
 - Borsomvang met normale, rustige respirasie
 - Borsomvang na maksimale inspirasie
 - Borsomvang na maksimale ekspirasie
- 6 Verdere borsmate is met die krompasser gemeet:
 - Borsbreedte
 - Borsdiepte
- 7 Hierna is die volgende omvangmate gemeet:
 - Die grootste omvang van die regterbo-arm — gestrek
 - Die grootste omvang van die regterbo-arm — gespan
 - Die grootste omvang van die regtervoorarm
 - Die grootste omvang van die regterdy
 - Die grootste omvang van die regterkuit
 - Die omvang van die buik op nawelhoogte
- 8 Met die skuifpasser is die twee kopmate gemeet:
 - Grootste lengte van die kop
 - Grootste breedte van die kop
- 9 Gewig.

IV ONTLEDING EN VERGELYKING VAN DIE LIGGAAMSMATE

A ABSOLUTE LIGGAAMSMATE

1 Liggaamslengte

Tabel 5

Gemiddelde liggaamslengte (M) van die ouderdomsgroepe

				Blank					Kleurling				
				Ouderdom in Jare									
				13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17
N		74	100	100	100	100	100	100	100	100	
M..		152.9	159.6	166.4	171.4	174.5	143.1	150.0	156.2	162.3	165.8
Min		139.3	140.8	134.6	157.5	157.5	128.9	131.3	139.3	145.5	152.0
Maks		165.5	177.4	188.0	185.0	188.4	162.2	171.7	176.3	190.4	182.2
s	6.23	8.44	8.81	6.12	6.72	6.44	8.55	7.78	7.70	5.77
v	4.07	5.29	5.29	3.57	3.85	4.50	5.70	4.98	4.78	3.48
±m		0.72	0.84	0.88	0.61	0.67	0.64	0.86	0.78	0.77	0.58
% Toename	..			(6.7	6.8)		(5.0	3.1)	(6.9	6.2)		(6.1	3.5)
				= 13.5			= 8.1		= 13.1			= 9.6	
				21.6 = 14.1%					22.7 = 15.9%				

Die gemiddelde liggaamslengte van die blanke seuns, tussen 13 en 17 jaar, is groter as dié van die Kleurlingseuns in elke ouderdomsgroep. Die verskille is soos volg:

Tabel 6

Verskille in gemiddelde liggaamslengte van die ouderdomsgroepe

13	14	15	16	17
9.8	9.6	10.2	9.1	8.7

Volgens die t-toets is al die verskille hoogs beduidend.

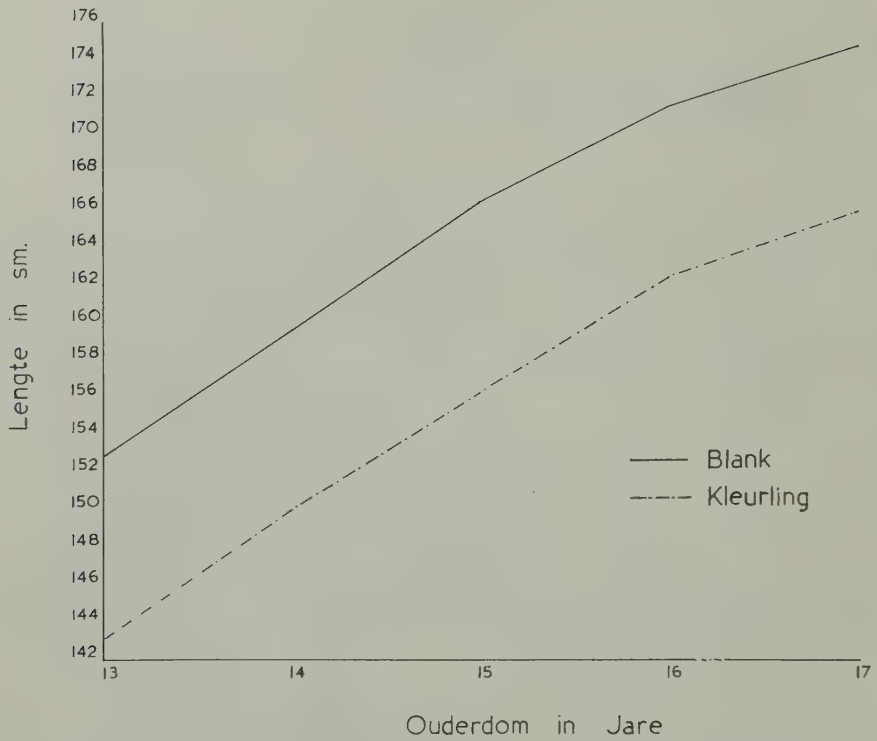
By die blanke seuns is die toename in liggaamslengte 21.6 sm. (14.1%) terwyl die toename by die Kleurlingseuns 22.9 sm. (15.7%) is (sien tabel 5).

Die blanke seuns toon 'n toename van 13.5 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 13.1 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (9.6 sm.) as by die blanke seuns (8.1 sm.)

Die snelheid van toename in lengtegroei neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. figuur 1).

Figuur 1

Grafiese voorstelling van die toename in liggaamslengte



2 Hoogte van die suprasternale

Tabel 7

Gemiddelde hoogte van suprasternale van die ouderdomsgroepe

			Blank					Kleurling				
			Ouderdom in Jare									
			13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17
N	74	100	100	100	100	100	100	100	100	80
M..	124.2	129.8	135.9	139.4	142.4	117.0	122.6	128.0	133.1	135.7
Min	112.0	115.0	120.8	123.0	128.3	104.9	105.6	114.5	120.2	123.6
Maks	135.5	146.4	153.9	152.9	157.6	133.5	143.0	145.6	158.2	150.1
s	5.29	7.27	7.27	5.79	6.11	5.68	7.59	6.64	6.59	4.91
v	4.26	5.60	5.35	4.15	4.29	4.85	6.19	5.16	4.95	3.61
±m	0.62	0.73	0.73	0.58	0.61	0.57	0.76	0.66	0.66	0.50
% Toename	..		(5.6	6.1)	(3.5	3.0)		(5.6	5.4)	(5.1	2.6)	
			= 11.7		= 6.5			= 11.0		= 7.7		
			18.2 = 14.7%					18.7 = 15.98%				

Die gemiddelde suprasternale hoogte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 8).

Tabel 8

Verskil in hoogte van suprasternale van die ouderdomsgroepe

13	14	15	16	17
7.2	7.2	7.9	6.3	6.7

Volgens die t-toets is al die verskille hoogs beduidend.

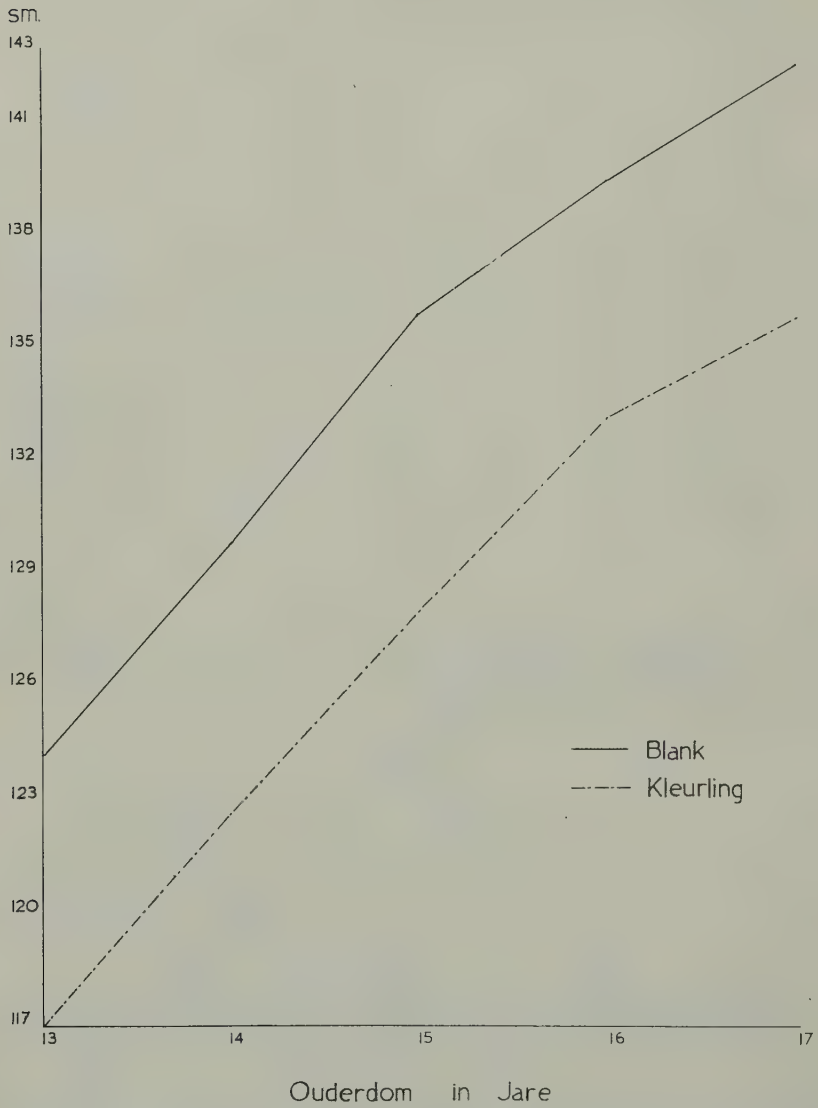
By die blanke seuns is die toename in suprasternale hoogte 18.2 sm. (14.7%) terwyl die toename by die Kleurlingseuns 18.7 sm. (15.98%) is (vgl. Tabel 7).

Die blanke seuns toon 'n toename van 11.7 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 11.0 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (7.7 sm.) as by die blanke seuns (6.5 sm.).

Die snelheid van toename in suprasternale hoogte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 2).

Figuur 2

Grafiese voorstelling van die toename in suprasternale hoogte



3 Hoogte van die nawel

Tabel 9

Gemiddelde van hoogte van nawel (M) van die ouderdomsgroepe

				Blank					Kleurling				
				Ouderdom in Jare									
				13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17 •
N		74	100	100	100	100	100	100	100	100	80
M..		92.8	96.9	101.5	104.1	105.7	86.3	90.8	94.9	98.7	100.5
Min		81.9	84.0	87.9	93.8	93.8	70.9	77.1	83.5	87.2	89.3
Maks		101.7	111.2	118.5	115.1	118.5	99.0	106.8	107.5	109.0	112.4
s	4.55	5.81	5.87	4.19	4.03	4.90	5.93	5.27	5.37	4.05
v	4.90	5.99	5.78	4.02	3.81	5.68	6.53	5.55	5.44	4.03
±m		0.53	0.58	0.59	0.42	0.40	0.49	0.59	0.53	0.54	0.45
% Toename				..	(4.1	4.6)	(2.6	1.6)	(4.5	4.1)	(3.8	1.8)	
					= 8.7		= 4.2		= 8.6		= 5.6		
				12.9 = 13.9%					14.2 = 16.5%				

Die gemiddelde nawelhoogte van die blanke seuns is groter in elke ouderdomsgroep (Tabel 10).

Tabel 10

Verskil in gemiddelde nawelhoogte van die ouderdomsgroepe

13	14	15	16	17
6.5	6.1	6.6	5.4	5.2

Volgens die t-toets is al die verskille hoogs beduidend.

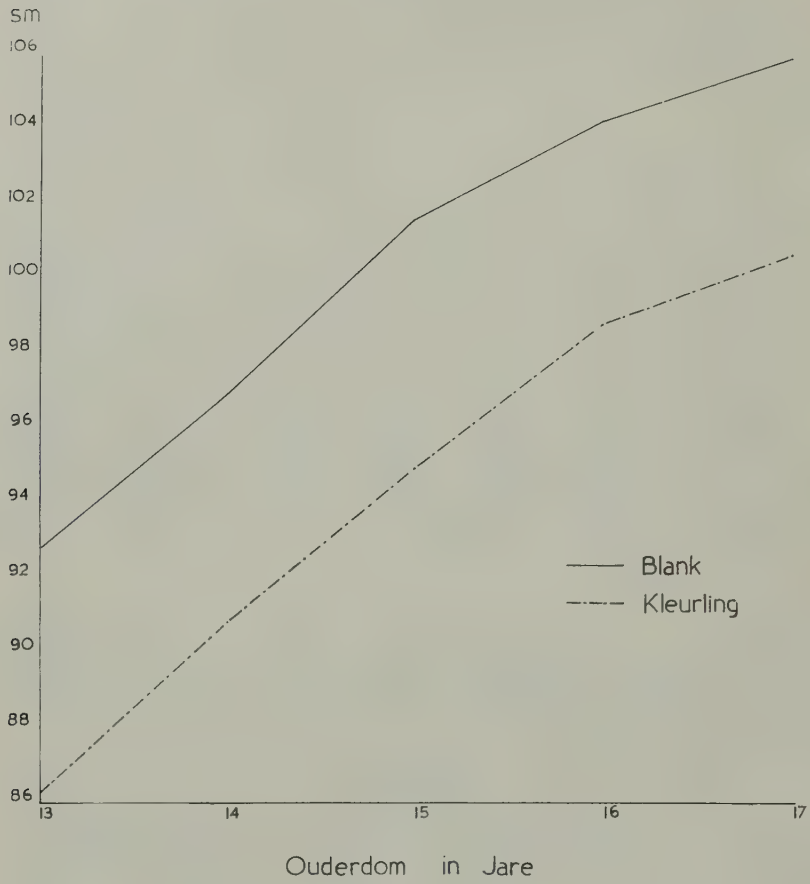
By die blanke seuns is die toename in nawelhoogte 12.9 sm. (13.9%) terwyl die toename by die Kleurlingseuns 14.2 sm. (16.5%) is (vgl. Tabel 9).

Die blanke seuns toon 'n toename van 8.7 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 8.6 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (5.6 sm.) as by die blanke seuns (4.2 sm.).

Die snelheid in toename in nawelhoogte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 3).

Figuur 3

Grafiese voorstelling van die toename in nawelhoogte



4 Hoogte van die symphysis

Tabel 11

Gemiddelde hoogte van symphysis hoogte van die ouderdomsgroepe

	Blank					Kleurling						
	Ouderdom in Jare											
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17 •		
N	74	100	100	100	100	100	100	100	100	80		
M.. ..	80.8	84.4	88.7	90.9	92.2	74.8	78.4	82.2	85.5	87.1		
Min.	71.0	74.6	77.5	82.8	81.5	65.8	67.2	72.2	75.4	77.5		
Maks.	87.7	98.6	104.4	104.1	104.3	85.9	93.3	92.3	104.3	95.2		
s	4.11	5.59	5.42	4.02	4.16	4.12	5.41	4.64	5.23	4.09		
v	5.08	6.62	6.12	4.42	4.51	5.51	6.90	5.64	6.12	4.70		
±m	0.48	0.56	0.54	0.40	0.42	0.40	0.54	0.46	0.52	0.46		
% Toename ..	(3.6	4.3)		(2.2	1.3)	(3.6	3.8)		(3.3	1.6)		
	= 7.9			= 3.5		= 7.4			= 4.9			
	11.4 = 14.1%					12.3 = 16.4%						

Die gemiddelde symphysis hoogte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 12).

Tabel 12

Verskil in symphysis hoogte van die ouderdomsgroepe

13	14	15	16	17
6.0	6.0	6.5	5.4	5.1

Volgens die t-toets is al die verskille hoogs beduidend.

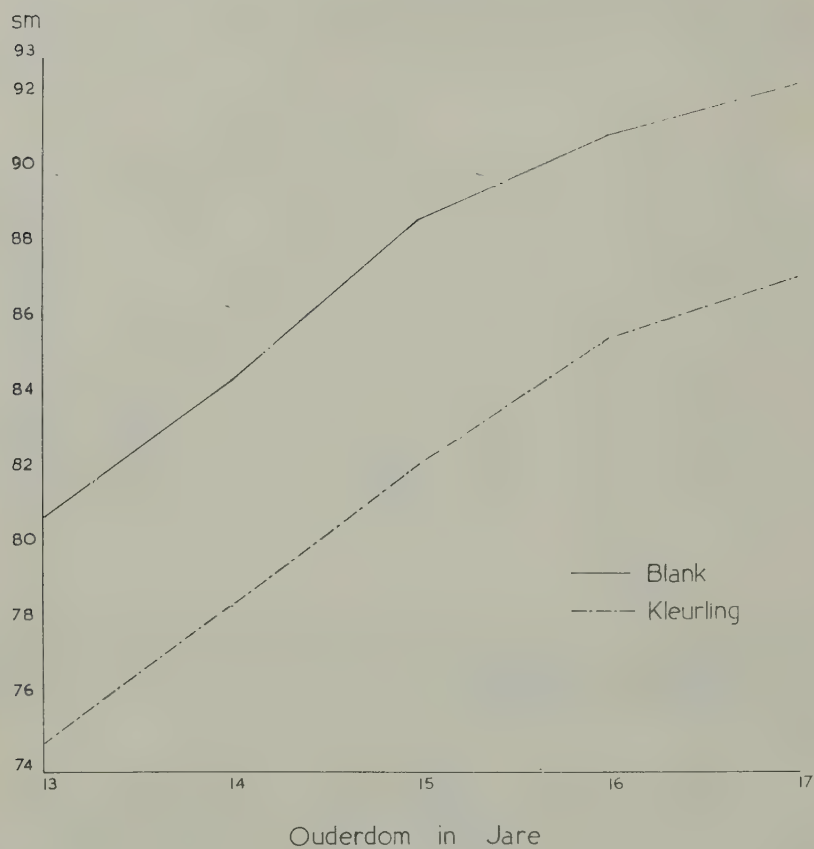
By die blanke seuns is die toename in symphysis hoogte 11.4 sm. (14.1%) terwyl die toename by die Kleurlingseuns 12.3 sm. (16.4%) is (vgl. Tabel 11).

Die blanke seuns toon 'n toename van 7.9 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 7.4 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (4.9 sm.) as by die blanke seuns (3.5 sm.).

Die reëlmatige toename in symphysis hoogte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 4).

Figuur 4

Grafiese voorstelling van die toename in symphysionhoogte



5 Hoogte van die regter-iliospinale

Tabel 13

Gemiddelde hoogte (M) van regter-iliospinale van die ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17 •	
N	74	100	100	100	100	100	100	100	100	80	
M.. .. .	86.3	90.1	94.4	96.5	97.6	80.7	84.0	88.0	91.6	93.0	
Min. .. .	75.2	78.6	77.2	87.8	87.5	71.1	71.5	77.6	81.1	82.3	
Maks. .. .	93.8	103.3	109.6	106.6	111.4	92.2	98.3	99.1	91.6	102.3	
s	4.14	6.01	5.48	4.16	4.78	4.52	5.42	5.01	5.16	4.07	
v	4.79	6.67	5.80	4.31	4.90	5.60	6.45	5.69	5.63	4.38	
±m	0.48	0.60	0.55	0.42	0.48	0.45	0.54	0.50	0.52	0.46	
% Toename ..	(3.8	4.3)		(2.1	1.1)	(3.3	4.0)		(3.6	1.4)	
	= 8.1			= 3.2		= 7.3			= 5.0		
	11.3 = 13.1%					12.3 = 15.2%					

Die gemiddelde iliospinale hoogte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 14).

Tabel 14

Verskil in iliospinale hoogte van ouderdomsgroepe

13	14	15	16	17
5.6	6.1	6.4	4.9	4.6

Volgens die t-toets is al die verskille hoogs beduidend.

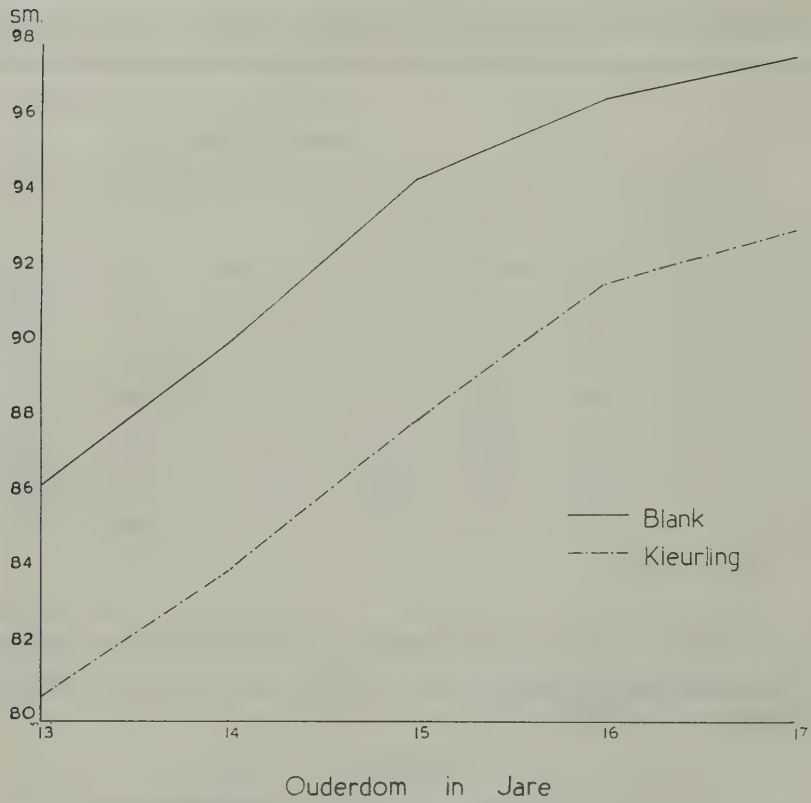
By die blanke seuns is die toename in iliospinale hoogte 11.3 sm. (13.1%) terwyl die toename by die Kleurlingseuns 12.3 sm. (15.2%) is (vgl. Tabel 13).

Die blanke seuns toon 'n toename van 8.1 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 7.3 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (5.0 sm.) as by die blanke seuns (3.2 sm.).

Die snelheid van toename in iliospinale hoogte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 5).

Figuur 5

Grafiese voorstelling van die toename in iliospinale hoogte



6 Hoogte van die regter-akromion (skouerhoogte)

Tabel 15

Gemiddelde skouerhoogte (M) van die ouderdomsgroepe

	Blank					Kleurling				
	Ouderdom in Jare									
	13	14	15	16	17	13	14	15	16	17
N	74	100	100	100	100	100	100	100	100	82
M.. ..	124.0	129.4	136.1	139.6	142.5	116.3	122.5	127.6	132.7	134.9
Min.	106.5	113.6	120.2	127.7	129.0	103.1	106.4	113.5	119.5	121.0
Maks.	136.1	146.5	155.7	151.7	159.9	131.9	141.1	145.7	156.6	149.8
s	6.07	8.08	7.44	5.35	6.18	5.64	7.40	6.59	6.91	5.06
v	4.89	6.24	5.46	3.83	4.34	4.84	6.04	5.16	5.21	3.75
±m	0.71	0.81	0.74	0.54	0.62	0.56	0.74	0.66	0.69	0.56
% Toename ..	(5.4	6.7)	(3.5	2.9)		(6.2	5.1)	(5.1	2.2)	
	= 12.1		= 6.4			= 11.3		= 7.3		
	18.5 = 14.9%					18.6 = 15.99%				

Die gemiddelde akromiale of skouerhoogte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 16).

Tabel 16

Verskil in die gemiddelde akromiale hoogte van die ouderdomsgroepe

13	14	15	16	17
7.7	6.9	8.5	6.9	7.6

Volgens die t-toets is al die verskille hoogs beduidend.

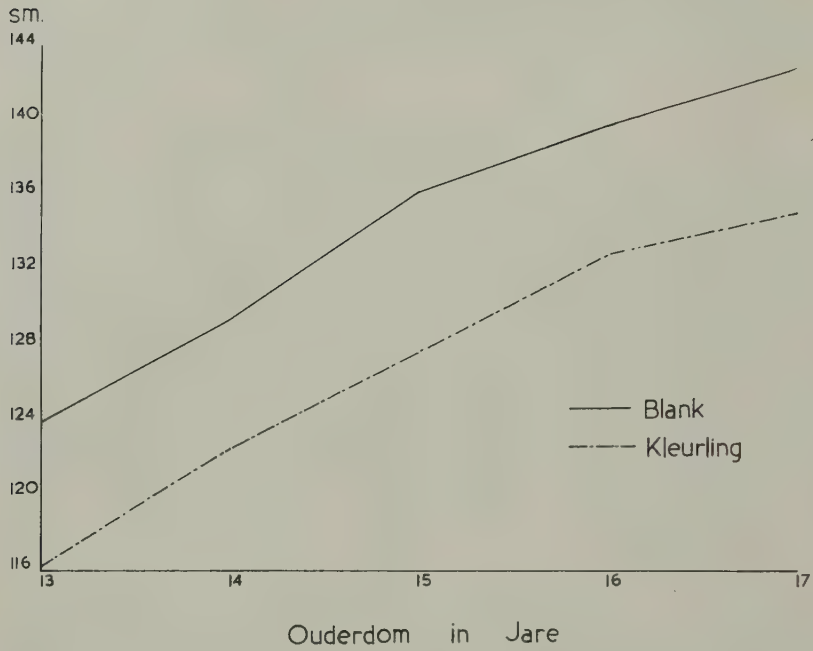
By die blanke seuns is die toename in akromiale hoogte 18.5 sm. (14.9%) terwyl die toename by die Kleurlingseuns 18.6 sm. (15.99%) is (vgl. Tabel 15).

Die blanke seuns toon 'n toename van 12.1 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 11.3 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (7.3 sm.) as by die blanke seuns (6.4 sm.).

Die snelheid van toename in akromiale hoogte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 6).

Figuur 6

Grafiese voorstelling van die toename in skouerhoogte



7 Sithoogte

Tabel 17

Gemiddelde sithoogte (M) van die ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	83	
M. . . .	78.2	82.0	85.5	88.2	90.9	73.8	77.0	80.0	82.9	84.8	
Min. . . .	72.4	71.2	76.3	78.8	81.5	66.7	68.2	71.4	73.3	75.7	
Maks. . . .	88.3	95.4	98.2	97.7	98.5	84.7	90.6	89.2	94.3	94.2	
s	3.17	4.32	4.56	3.61	3.57	3.16	4.31	4.19	4.09	3.35	
v	4.05	5.27	5.33	4.09	3.92	4.28	5.60	5.24	4.93	3.95	
±m	0.37	0.43	0.46	0.36	0.36	0.32	0.43	0.42	0.41	0.37	
% Toename ..	(3.8	3.5)		(2.7	2.7)	(3.2	3.0)		(2.9	1.9)	
	= 7.3			= 5.4		= 6.2			= 4.8		
	12.7 = 16.2%					11.0 = 14.91%					

Die gemiddelde sithoogte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 18).

Tabel 18

Verskil in die gemiddelde sithoogte van die ouderdomsgroepe

13	14	15	16	17
4.4	5.0	5.5	5.3	6.1

Volgens die t-toets is al die verskille hoogs beduidend.

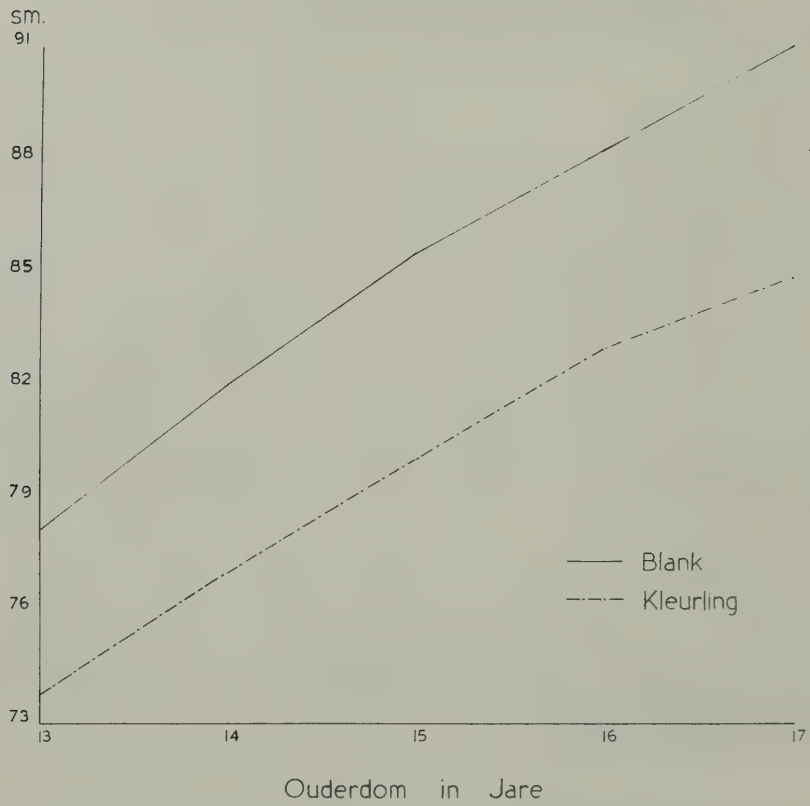
By die blanke seuns is die toename in sithoogte 12.7 sm. (16.2%) terwyl die toename by die Kleurlingseuns 11.0 sm. (14.9%) is (vgl. Tabel 17).

Die blanke seuns toon 'n toename van 7.3 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 6.2 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (5.4 sm.) as by die Kleurlingseuns (4.8 sm.).

Die snelheid van toename in sithoogte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers afneem na die 16de jaar (vgl. Figuur 7).

Figuur 7

Grafiese voorstelling van die toename in sithoogte



8 Voorste romplengte

Tabel 19

Gemiddelde voorste romplengte (M) van die ouderdomsgroepe

			Blank					Kleurling					
			Ouderdom in Jare										
			13 •	14 •	15 •	16 •	17 •	13 •	14 •	15 •	16 •	17 •	
N	74	100	100	100	100	100	100	100	80		
M..	43.3	45.2	47.4	48.4	50.1	41.6	44.0	45.7	47.7	48.5	
Min.	38.4	33.9	40.8	38.0	43.5	37.3	38.2	38.7	41.1	42.2	
Maks.	48.3	55.2	55.9	54.2	57.8	50.8	50.8	54.2	53.9	55.7	
s	2.24	3.01	3.70	3.16	2.54	2.30	2.88	3.05	2.53	2.29	
v	5.17	6.66	7.81	6.52	5.07	5.53	6.55	6.67	5.30	4.72	
±m	0.26	0.30	0.37	0.32	0.25	0.23	0.29	0.31	0.25	0.26	
% Toename	..		(1.9	2.2)		(1.0	1.7)		(2.4	1.7)		(2.0	0.8)
			= 4.1			= 2.7			= 4.1			= 2.8	
			6.8 = 15.7%					6.9 = 16.6%					

Die gemiddelde voorste romplengte van die blanke seuns is groter in elke ouderdomsgroep. (vgl. Tabel 20).

Tabel 20

Verskil in die gemiddelde voorste romplengte van die ouderdomsgroepe

13	14	15	16	17
1.7	1.2	1.7	0.7	1.6

Volgens die t-toets is die verskille in romplengte by 13, 14, 15 en 17 jaar hoogs beduidend, terwyl die verskil in die 16-jarige ouderdomsgroep beduidend by die 5%-grens is.

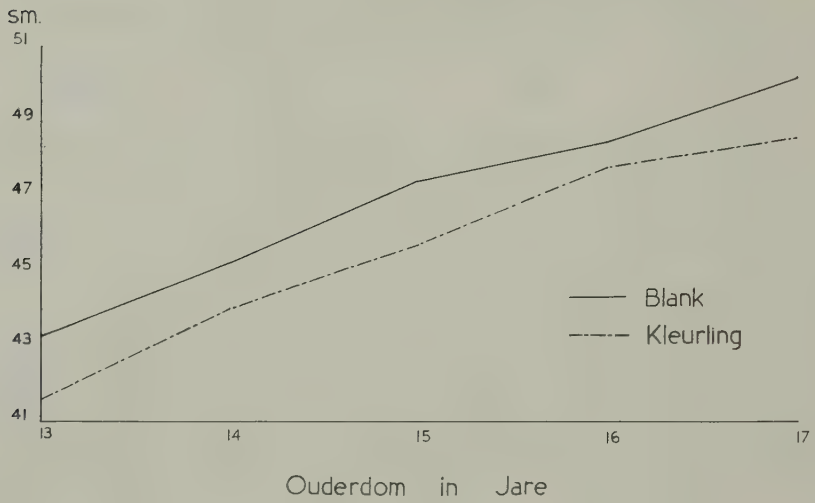
By die blanke seuns is die toename in voorste romplengte 6.8 sm. (15.7%) terwyl die toename by die Kleurlingseuns 6.9 sm. (16.6%) is (vgl. Tabel 19).

Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (2.8 sm.) as by die blanke seuns (2.7 sm.).

Die toename in voorste romplengte geskied meer reëlmagig by die Kleurlingseuns (vgl. Figuur 8).

Figuur 8

Grafiese voorstelling van die toename in voorste romplengte



9 Spanwydte van die arms

Tabel 21

Gemiddelde spanwydte (M) van die arms van die ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	100	83
M.. ..	156.6	164.6	173.4	177.6	182.0	149.1	156.3	163.9	170.8	175.2	
Min.	141.1	140.8	150.2	161.7	165.0	135.3	134.8	144.1	151.7	158.5	
Maks.	169.5	192.6	198.0	196.7	200.3	168.8	178.5	188.5	200.5	195.1	
s	6.57	10.01	9.97	7.10	7.97	7.40	9.63	8.98	8.81	7.13	
v	4.13	6.11	5.74	3.99	4.38	4.96	6.16	5.48	5.16	4.07	
±m	0.76	1.00	1.00	0.71	0.80	0.74	0.96	0.90	0.88	0.78	
% Toename ..	(8.0	8.8)	(4.2	4.4)		(7.2	7.6)	(6.9	4.4)		
	= 16.8		= 8.6			= 14.8		= 11.3			
	25.4 = 16.2%					26.1 = 17.5%					

Die gemiddelde spanwydte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 22).

Tabel 22

Verskil in die gemiddelde spanwydte van die ouderdomsgroepe

13	14	15	16	17
7.5	8.3	9.5	6.8	6.8

Volgens die t-toets is al die verskille hoogs beduidend.

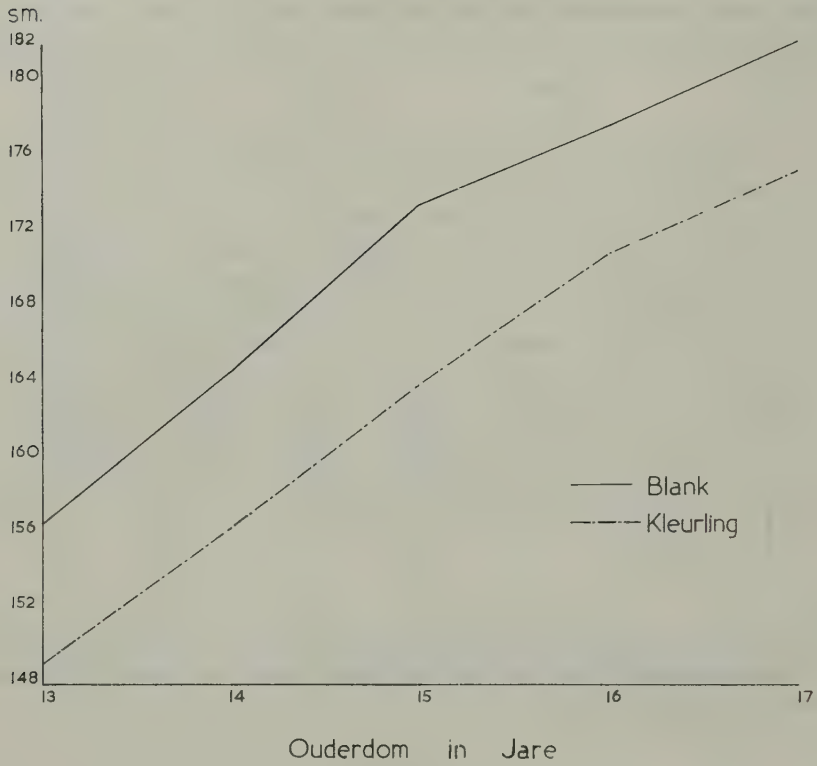
By die blanke seuns is die toename in spanwydte 25.4 sm. (16.2%) terwyl die toename by die Kleurlingseuns 26.1 sm. (17.5%) is (sien Tabel 21).

Die blanke seuns toon 'n toename van 16.8 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 14.8 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (11.3 sm.) as by die blanke seuns (8.6 sm.).

Die snelheid van toename in spanwydte neem by die blanke seuns eers merkbaar af na die 16de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 9).

Figuur 9

Grafiese voorstelling van die toename in spanwydte van die arms



10 Lengte van die regterarm

Tabel 23

Gemiddelde lengte (M) van regterarm van die ouderdomsgroepe

	Blank					Kleurling				
	Ouderdom in Jare									
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17 •
N	74	100	100	100	100	100	100	100	100	80
M.. .. .	67.0	70.7	74.4	76.3	78.3	63.6	67.7	70.3	73.3	74.3
Min. .. .	51.4	59.4	64.8	68.8	70.0	56.4	57.7	62.8	64.1	66.3
Maks. .. .	73.9	83.3	86.1	83.6	87.2	72.3	78.0	80.8	88.2	84.4
s	4.03	4.83	4.46	3.13	3.78	3.55	4.38	3.80	4.14	3.35
v	6.02	6.83	5.99	4.10	4.82	5.58	6.47	5.41	5.65	4.51
± m	0.47	0.48	0.45	0.31	0.38	0.36	0.44	0.38	0.41	0.37
% Toename ..	(3.7	3.7)	(1.9	2.0)		(4.1	2.6)	(3.0	1.0)	
	= 7.4		= 3.9			= 6.7		= 4.0		
	11.3 = 16.87%					10.7 = 16.82%				

Die gemiddelde armlengte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 23).

Tabel 24

Verskil in die gemiddelde lengte van regterarm van die ouderdomsgroepe

13	14	15	16	17
3.4	3.0	4.1	3.0	4.0

Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in armlengte 11.3 sm. (16.87%) terwyl die toename by die Kleurlingseuns 10.7 sm. (16.82%) is (vgl. Tabel 23).

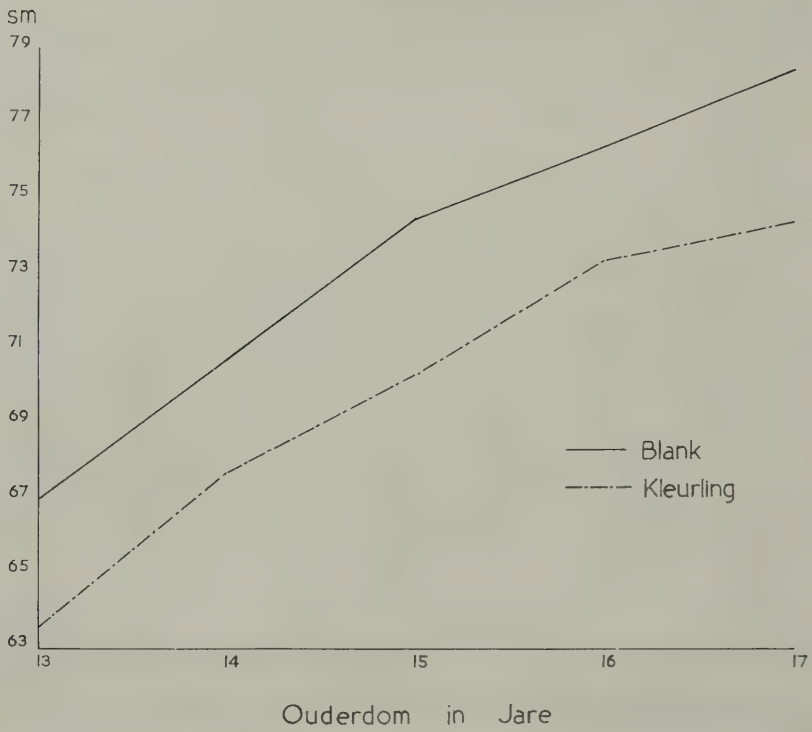
Die blanke seuns toon 'n toename van 7.4 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 6.7 sm. is.

Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (4.0 sm.) as by die blanke seuns (3.9 sm.).

Die armlengte neem by die blanke seuns meer reëlmatig toe as by die Kleurlingseuns (vgl. Figuur 10).

Figuur 10

Grafiese voorstelling van die toename in armlengte



11 Lengte van regterbeen

Tabel 25

Gemiddelde lengte (M) van regterbeen van die ouderdomsgroepe

			Blank					Kleurling					
			Ouderdom in Jare										
			13	•	14	•	15	•	16	•	17	•	
N	74	100	100	100	100	100	100	100	100	100	80
M..	84.0	88.0	92.0	94.4	95.7	78.3	82.0	85.7	89.0	90.6	
Min.	74.5	76.9	81.0	86.3	85.0	70.6	70.7	75.7	78.9	81.0	
Maks.	91.2	101.1	107.9	107.6	107.8	89.4	96.8	95.8	107.8	98.7	
s	3.92	5.52	5.40	4.03	4.52	4.33	5.41	4.65	5.23	4.03	
v	4.67	6.27	5.92	4.27	4.72	5.53	6.60	5.43	5.88	4.44	
—m	0.46	0.55	0.54	0.40	0.45	0.43	0.54	0.47	0.52	0.45	
% Toename	..		(4.0	4.0)	(2.4	1.3)		(3.7	3.7)	(3.3	1.6)		
			= 8.0		= 3.7			= 7.4		= 4.9			
			11.7 = 13.9%					12.3 = 15.7%					

Die gemiddelde beenlengte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 26).

Tabel 26

Verskil in die gemiddelde beenlengte van die ouderdomsgroepe

13	14	15	16	17
5.7	6.0	6.3	5.4	5.1

Volgens die t-toets is al die verskille hoogs beduidend.

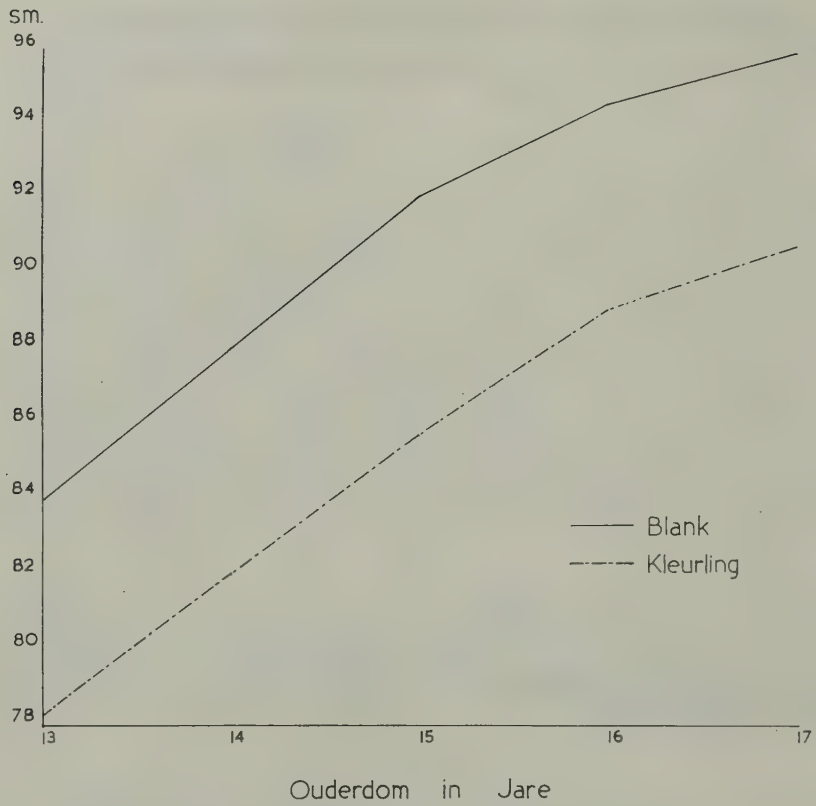
By die blanke seuns is die toename in beenlengte 11.7 sm. (13.9%) terwyl die toename by die Kleurlingseuns 12.3 sm. (15.7%) is (vgl. Tabel 25).

Die blanke seuns toon 'n toename van 8.0 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 7.4 sm. is. Die toename vanaf 15-17 jaar is groter by die Kleurlingseuns (4.9 sm.) as by die blanke seuns (3.7 sm.).

Die snelheid van toename in beenlengte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 11).

Figuur 11

Grafiese voorstelling van die toename in beenlengte



12 Skouerbreedte (afstand tussen akromia)

Tabel 27

Gemiddelde skouerbreedte (M) van die ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	80	
M.. .. .	33.3	34.9	36.2	37.8	39.3	31.7	33.3	35.0	36.6	37.6	
Min. .. .	28.8	29.9	32.0	32.2	34.8	28.0	28.8	30.3	31.4	33.2	
Maks. .. .	37.4	39.7	41.5	43.0	44.9	36.7	39.4	40.0	41.3	43.5	
s	1.80	2.08	2.38	2.39	2.03	1.72	2.11	2.14	2.07	1.92	
v	5.41	5.95	6.56	6.32	5.15	5.42	6.34	6.11	5.66	5.11	
±m	0.11	0.21	0.24	0.24	0.20	0.17	0.21	0.21	0.21	0.21	
% Toename ..	(1.6 1.3) (1.6 1.5)					(1.6 1.7) (1.6 1.0)					
	= 2.9 = 3.1					= 3.3 = 2.6					
	6.0 = 18.0%					5.9 = 18.6%					

Die gemiddelde skouerbreedte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 28).

Tabel 28

Verskil in die gemiddelde skouerbreedte van die ouderdomsgroepe

13	14	15	16	17
1.6	1.6	1.2	1.2	1.7

Volgens die t-toets is al die verskille hoogs beduidend.

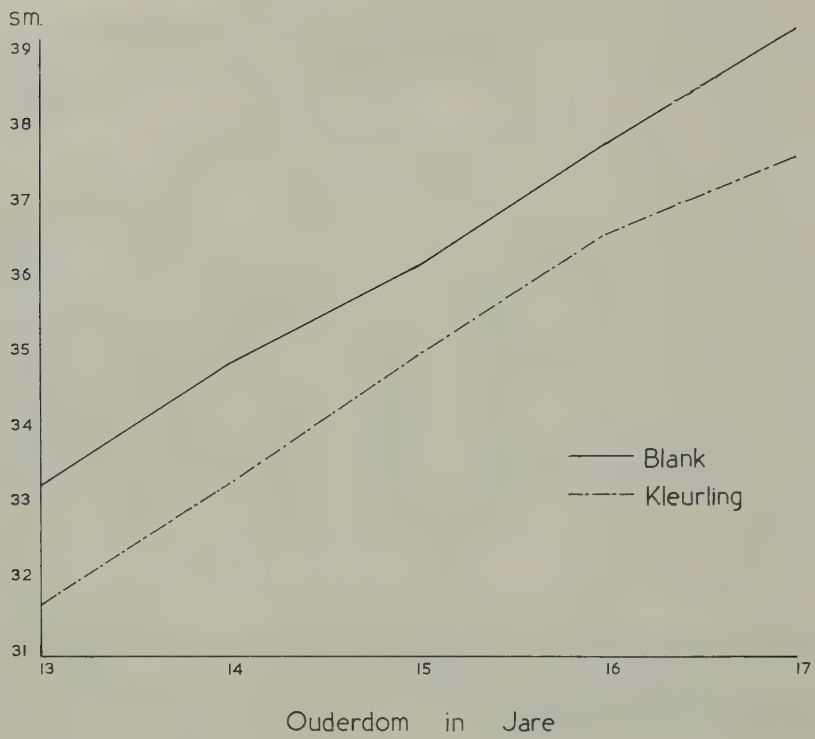
By die blanke seuns is die toename in skouerbreedte 6.0 sm. (18.0%) terwyl die toename by die Kleurlingseuns 5.9 sm. (18.6%) is (vgl. Tabel 27).

Die blanke seuns toon 'n toename van 2.9 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 3.3 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (3.1 sm.) as by die Kleurlingseuns (2.6 sm.).

Die toename in skouerbreedte geskied reëlmatig by albei groepe (vgl. Figuur 12).

Figuur 12

Grafiese voorstelling van die toename in skouerbreedte



13 Mammillare breedte
(afstand tussen borspapille)

Tabel 29

Gemiddelde Mammillare breedte (M) van die ouderdomsgroepe

	Blank					Kleurling				
	Ouderdom in Jare									
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17 •
N	74	100	100	100	100	100	100	100	100	80
M.. .. .	16·7	17·3	18·3	19·5	20·3	15·9	16·4	17·6	18·3	18·6
Min. .. .	14·2	14·0	15·1	16·2	16·6	13·4	13·6	14·1	15·4	16·4
Maks. .. .	20·9	21·0	22·3	25·0	26·6	19·3	19·0	20·9	22·5	21·3
s	1·35	1·43	1·52	1·43	1·72	1·21	1·26	1·59	1·44	1·23
v	8·08	8·27	8·31	7·33	8·47	7·67	7·68	9·03	7·87	6·61
±m	0·16	0·14	0·15	0·14	0·17	0·12	0·13	0·16	0·14	0·14
% Toename ..	(0·6	1·0)	(1·2	0·8)		(0·5	1·2)	(0·7	0·3)	
	= 1·6		= 2·0			= 1·7		= 1·0		
	3·6 = 21·6%					2·7 = 17·0%				

Die gemiddelde mammillare breedte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 30).

Tabel 30

Verskil in die gemiddelde Mammillare breedte van die ouderdomsgroepe

13	14	15	16	17
0.8	0.9	0.7	1.2	1.7

Volgens die t-toets is al die verskille hoogs beduidend.

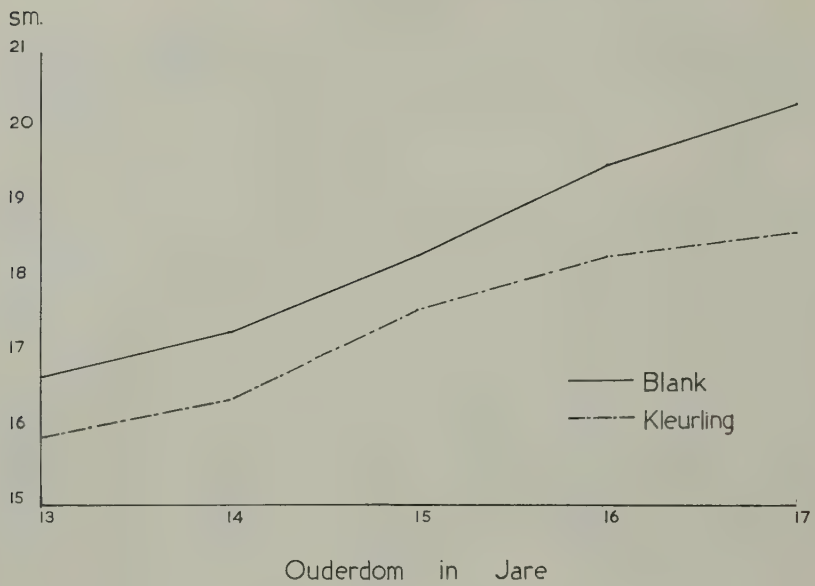
By die blanke seuns is die toename in mammillare breedte 3.6 sm. (21.6%) terwyl die toename by die Kleurlingseuns 2.7 sm. (17.0%) is (vgl. Tabel 29).

Die blanke seuns toon 'n toename van 1.6 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 1.7 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (2.0 sm.) as by die Kleurlingseuns (1.0 sm.)

Die toename in die mammillare breedte is effens meer onreëlmatig by die Kleurlingseuns (vgl. Figuur 13).

Figuur 13

Grafiese voorstelling van toename in mammillare breedte



14 Bekkenbreedte

Tabel 31

Gemiddelde bekkenbreedte (M) van die ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	100	80
M.. ..	24.2	25.2	26.3	27.1	27.9	21.8	23.1	24.2	25.1	25.4	
Min.	20.9	21.9	22.1	23.4	22.8	18.2	18.4	20.9	21.5	21.1	
Maks.	26.7	31.2	31.0	37.0	33.2	24.7	27.8	28.9	28.9	29.0	
s'	1.39	1.88	1.87	1.88	1.87	1.18	1.72	1.60	1.74	1.55	
v	5.74	7.46	7.12	6.94	6.68	5.41	7.45	6.61	6.93	6.10	
±m	0.16	0.19	0.19	0.19	0.19	0.12	0.17	0.16	0.17	0.17	
% Toename ..	(1.0	1.1)	(0.8	0.8)		(1.3	1.1)	(0.9	0.3)		
	= 2.1		= 1.6			= 2.4		= 1.2			
	3.7 = 15.3%					3.6 = 16.5%					

Die gemiddelde bekkenbreedte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 32).

Tabel 32

Verskil in die gemiddelde bekkenbreedte van die ouderdomsgroepe

13	14	15	16	17
2.4	2.1	2.1	2.0	2.5

Volgens die t-toets is al die verskille hoogs beduidend.

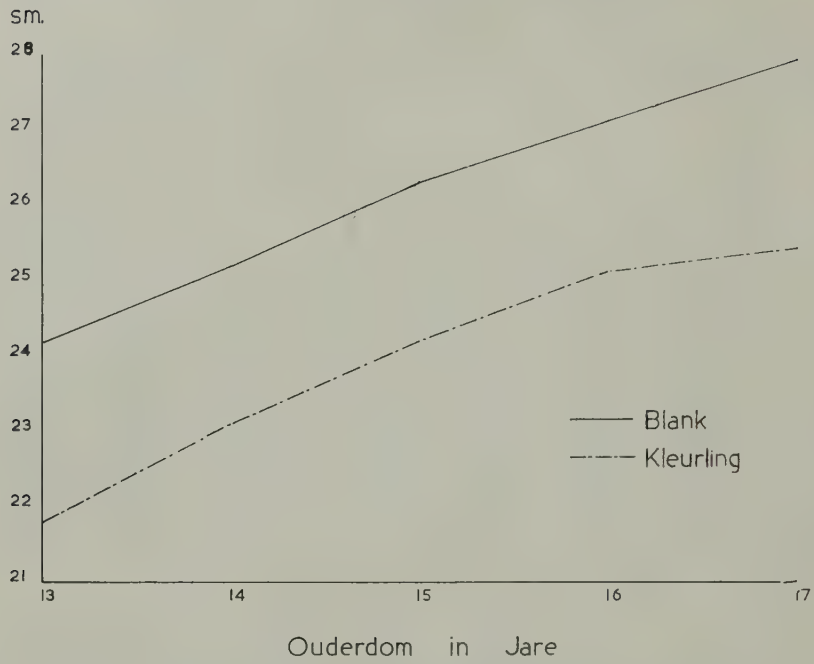
By die blanke seuns is die toename in bekkenbreedte 3.7 sm. (15.3%) terwyl die toename by die Kleurlingseuns 3.6 sm. (16.5%) is (vgl. Tabel 31).

Die blanke seuns toon 'n toename van 2.1 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 2.4 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (1.6 sm.) as by die Kleurlingseuns (1.2 sm.).

Die snelheid van toename in bekkenbreedte neem by die blanke seuns eers merkbaar af na die 15de jaar terwyl dit in die geval van die Kleurlingseuns eers na die 16de jaar afneem (vgl. Figuur 14).

Figuur 14

Grafiese voorstelling van die toename in bekkenbreedte



15 *Iliospinale breedte*

Tabel 33

Gemiddelde iliospinale breedte (M) van die ouderdomsgroepe

			Blank					Kleurling					
			Ouderdom in Jare										
			13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	80	
M..	19.9	20.2	21.9	22.0	22.8	17.8	18.4	19.5	19.9	20.2	
Min.	16.4	16.0	17.1	17.0	18.7	15.0	14.5	16.4	16.2	16.6	
Maks.	23.6	24.6	26.0	27.1	28.5	20.1	22.3	23.7	24.2	23.2	
s	1.51	1.75	1.75	1.78	2.24	1.17	1.62	1.48	1.76	1.61	
v	7.59	8.66	7.97	8.09	9.81	6.57	8.80	7.64	8.79	7.97	
±m	0.18	0.18	0.18	0.18	0.22	0.12	0.16	0.15	0.18	0.18	
% Toename	..		(0.3	1.7)		(0.1	0.8)		(0.6	1.1)		(0.4	0.3)
			= 2.0			= 0.9			= 1.7			= 0.7	
			2.9 = 14.6%						2.4 = 13.5%				

Die gemiddelde iliospinale breedte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 34).

Tabel 34

Verskil in die gemiddelde iliospinale breedte van die ouderdomsgroepe

13	14	15	16	17
2.1	1.8	2.4	2.1	2.6

Volgens die t-toets is al die verskille hoogs beduidend.

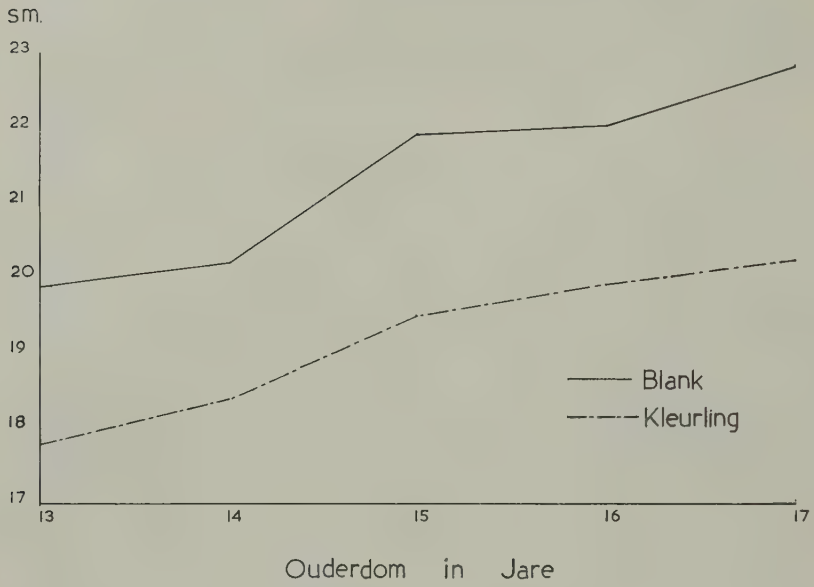
By die blanke seuns is die toename in iliospinale breedte 2.9 sm. (14.6%) terwyl die toename by die Kleurlingseuns 2.4 sm. (13.5%) is (vgl. Tabel 33).

Die blanke seuns toon 'n toename van 2.0 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 1.7 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (0.9 sm.) as by die Kleurlingseuns (0.7 sm.)

Die toename in iliospinale breedte geskied taamlik onreëlmatig by albei groepe (vgl. Figuur 15).

Figuur 15

Grafiese voorstelling van die toename in iliospinale breedte



16(a) Borsomvang met normale rustige respirasie

Tabel 35

Gemiddelde borsomvang (M) van die ouderdomsgroepe

				Blank					Kleurling						
				Ouderdom in Jare											
				13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•	
N		74	100	100	100	100	100	100	100	100	100	80	
M..		74.0	77.6	81.5	86.8	90.4	68.7	71.7	76.0	79.3	81.2		
Min.		64.0	69.5	68.0	74.0	78.0	63.0	63.0	67.0	67.5	71.5		
Maks.		87.3	89.5	92.7	113.0	109.0	80.7	84.0	88.2	89.0	90.2		
s	4.62	5.01	5.13	5.72	5.65	3.80	4.64	4.65	4.88	4.13		
v	6.24	6.46	6.29	6.59	6.25	5.53	6.47	6.12	6.15	5.09		
±m		0.54	0.50	0.51	0.57	0.57	0.38	0.46	0.47	0.49	0.41		
% Toename				..	(3.6	3.9)	(5.3	3.6)	(3.0	4.3)	(3.3	1.9)			
					= 7.5		= 8.9		= 7.3		= 5.2				
					16.4 = 22.2%					12.5 = 18.2%					

Die gemiddelde normale borsomvang van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 36).

Tabel 36

Verskil in gemiddelde borsomvang van die ouderdomsgroepe

13	14	15	16	17
5.3	5.9	5.5	7.5	9.2

Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in borsomvang 16.4 sm. (22.2%) terwyl die toename by die Kleurlingseuns 12.5 sm. (18.2%) is (vgl. Tabel 35).

Die blanke seuns toon 'n toename van 7.5 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 7.3 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (8.9 sm.) as by die Kleurlingseuns (5.2 sm.).

16(b) Borsomvang met maksimale inspirasie

Tabel 37

Gemiddelde Borsomvang met maksimale inspirasie

			Blank					Kleurling				
			Ouderdom in Jare									
			13	14	15	16	17	13	14	15	16	17
N	74	100	100	100	100	100	100	100	100	80
M..	77.5	81.5	85.6	90.6	94.3	71.9	75.4	79.2	82.6	84.6
Min.	69.0	72.0	73.0	79.0	82.5	65.1	67.2	68.5	71.4	75.1
Maks.	89.6	94.4	97.3	115.2	112.5	82.5	86.5	90.5	92.5	92.5
s	4.28	4.81	5.20	5.64	5.73	3.93	4.54	4.86	4.63	4.02
v	5.52	5.09	6.07	6.23	6.06	5.46	6.02	6.14	5.61	4.75
±m	0.50	0.48	0.52	0.56	0.57	0.39	0.45	0.49	0.46	0.45
% Toename	..		(4.0	4.1)	(5.0	3.7)		(3.5	3.8)	(3.4	2.0)	
			= 8.1		= 8.7			= 7.3		= 5.4		
			16.8 = 21.7%					12.7 = 17.7%				

Die gemiddelde borsomvang, tydens diep inspirasie, van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 38).

Tabel 38

Verskil in die gemiddelde borsomvang met maksimale inspirasie van die ouderdomsgroepe

13	14	15	16	17
5.6	6.1	6.4	8.0	9.7

Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in borsomvang 16.8 sm. (21.7%) terwyl die toename by die Kleurlingseuns 12.7 sm. (17.7%) is (vgl. Tabel 37).

Die blanke seuns toon 'n toename van 8.1 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 7.3 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (8.7 sm.) as by die Kleurlingseuns (5.4 sm.).

16(c) *Borsomvang na ekspirasie*

Tabel 39

Gemiddelde borsomvang (M) met maksimale ekspirasie van die ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	80	
M.. ..	72.1	75.9	79.6	84.6	88.1	66.8	70.1	74.2	77.5	79.1	
Min.	62.0	68.0	65.5	70.5	76.9	60.8	61.0	63.5	64.4	70.0	
Maks.	86.9	87.8	92.2	111.5	107.0	79.3	81.3	85.0	87.2	88.8	
s	4.72	4.94	5.22	5.71	5.57	3.81	4.67	4.61	4.77	3.96	
v	6.55	6.51	6.56	6.75	6.32	5.70	6.65	6.21	6.15	5.01	
±m	0.47	0.49	0.52	0.57	0.56	0.38	0.47	0.46	0.48	0.44	
% Toename ..	(3.8	3.7)	(5.0	3.5)		(3.3	4.1)	(3.3	1.6)		
	= 7.5		= 8.5			= 7.4		= 4.9			
	16.0 = 22.2%					12.3 = 18.4%					

Die gemiddelde borsomvang, na ekspirasie, van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 40).

Tabel 40

Verskil in die gemiddelde borsomvang met maksimale ekspirasie van die ouderdomsgroepe

13	14	15	16	17
5.3	5.8	5.4	7.1	9.0

Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in borsomvang 16.0 sm. (22.2%) terwyl die toename by die Kleurlingseuns 12.3 sm. (18.4%) is (vgl. Tabel 39).

Die blanke seuns toon 'n toename van 7.5 sm. van 13-15 jaar terwyl die toename by die Kleurlingseuns 7.4 sm. is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (8.5 sm.) as by die Kleurlingseuns (4.9 sm.).

16(d) Borsuitsetting

Die gemiddelde maksimale borsuitsetting van die blanke seuns is baie effens groter as die van die Kleurlingseuns (vgl. Tabel 41).

Tabel 41

Gemiddelde maksimale borsuitsetting van die ouderdomsgroepe

Borsuitsetting			
Jare	Blanke	Kleurling	Verskil
13	5.4	5.1	0.3
14	5.6	5.3	0.3
15	6.0	5.0	1.0
16	6.0	5.1	0.9
17	6.2	5.5	0.7

In teenstelling met die borsuitsetting van die Kleurlingseuns van 13-17 jaar, wat baie konstant bly, word die borsuitsetting by die blanke seuns van 13-17 jaar groter. Dienooreenkomstig word die verskil in borsuitsetting groter by die blanke seun van 13-17 jaar.

17 Borsbreedte (Transversale deursnee)

Tabel 42

Gemiddelde borsbreedte (M) van die ouderdomsgroepe

	Blank					Kleurling				
	Ouderdom in Jare									
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17 •
N	74	100	100	100	100	100	100	100	100	82
M. . . .	22.3	23.1	24.7	25.5	26.6	21.1	21.8	22.9	23.7	24.4
Min. . . .	18.7	20.0	21.3	21.4	21.1	18.5	19.3	19.2	19.1	20.3
Maks. . . .	29.1	28.5	29.5	32.5	30.2	24.2	24.3	26.8	27.3	27.5
s	1.71	1.71	1.86	1.87	1.79	1.17	1.30	1.59	1.67	1.39
v	7.67	7.40	7.53	7.33	6.73	5.21	5.94	6.94	7.05	5.70
±m	0.20	0.17	0.19	0.19	0.18	0.12	0.13	0.16	0.17	0.15
% Toename ..	0.8 1.6 0.8 1.1					0.7 1.1 0.8 0.7				
	4.3 = 19.3%					3.3 = 15.6%				

Die gemiddelde borsbreedte, op die hoogte van die vierde rib, van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 43).

Tabel 43

Verskil in gemiddelde borsbreedte van die ouderdomsgroepe

13	14	15	16	17
1.2	1.3	1.8	1.8	2.2

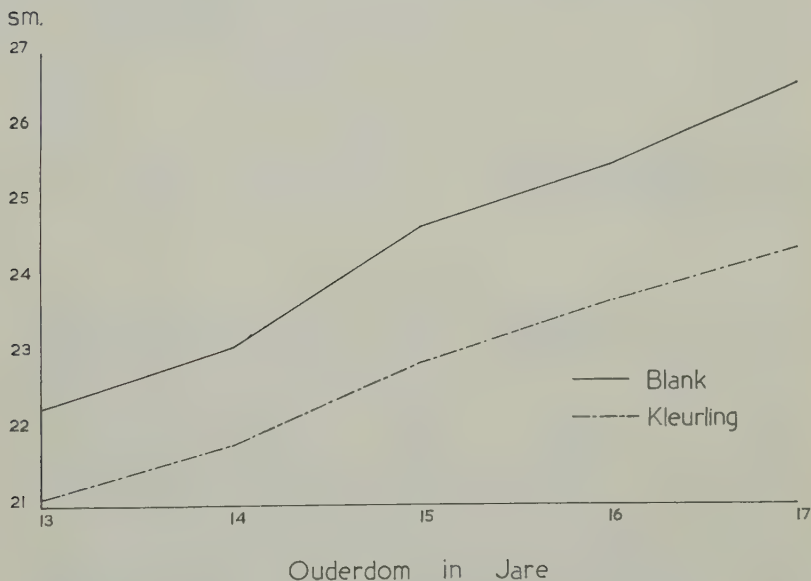
Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in borsbreedte 4.3 sm. (19.3%) terwyl die toename by die Kleurlingseuns 3.3 sm. (15.6%) is (vgl. Tabel 42).

Die toename in borsbreedte geskied meer reëlmatig by die Kleurlingseuns (vgl. Figuur 16).

Figuur 16

Grafiese voorstelling van die toename in borsbreedte



18 Borsdiepte (*Sagittale deursnee*)

Tabel 44

Gemiddelde borsdiepte (M) van die ouderdomsgroepe

	Blank					Kleurling						
	Ouderdom in Jare											
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17 •		
N	74	100	100	100	100	100	100	100	100	82		
M.. ..	16.2	17.0	17.7	18.8	19.5	14.6	15.1	15.7	16.3	16.7		
Min.	13.0	14.4	14.7	15.5	15.0	12.1	12.2	13.3	13.2	14.5		
Maks.	19.7	19.9	22.2	24.9	23.5	17.3	19.2	19.2	19.0	19.3		
s	1.25	1.42	1.50	1.68	1.70	1.02	1.32	1.23	1.17	1.22		
v	7.72	8.35	8.49	8.94	8.72	6.98	8.75	7.83	7.18	7.31		
±m	0.15	0.14	0.15	0.17	0.17	0.10	0.13	0.12	0.12	0.13		
% Toename ..	0.8 0.7 1.1 0.7					0.5 0.6 0.6 0.4						
	3.3 = 20.4%					2.1 = 14.4%						

Die gemiddelde borsdiepte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 45).

Tabel 45

Verskil in die gemiddelde borsdiepte van die ouderdomsgroepe

13	14	15	16	17
1.6	1.9	2.0	2.5	2.8

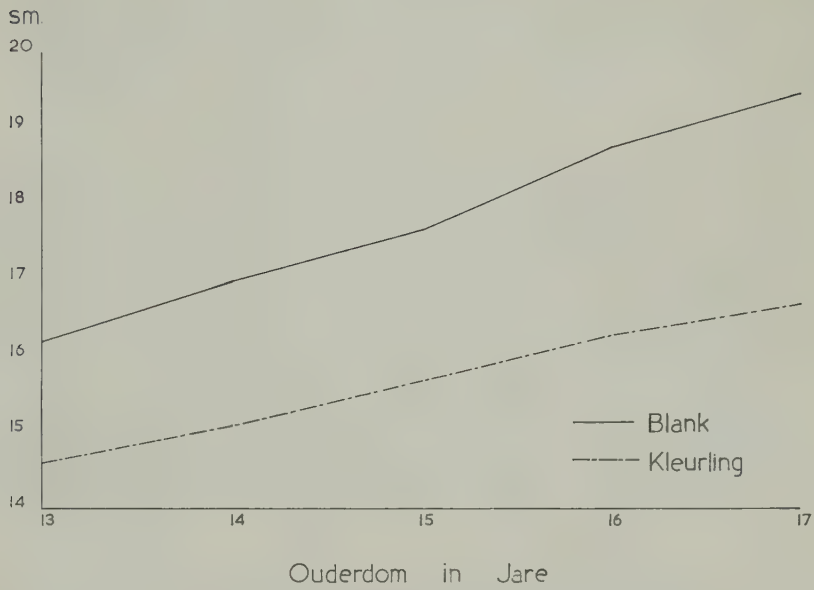
Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in borsdiepte 3.3 sm. (20.4%) terwyl die toename by die Kleurlingseuns 2.1 sm. (14.4%) is (vgl. Tabel 44).

Soos gesien by die toename in borsbreedte, geskied die toename in borsdiepte ook hier meer reëlmattig by die Kleurlingseuns (vgl. Figuur 17).

Figuur 17

Grafiese voorstelling van die toename in borsdiepte



19(a) Grootste omvang van die regterbo-arm — gestrek

Tabel 46

Gemiddelde grootste omvang van die regterbo-arm van die ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	14	15	16	17	13	14	15	16	17	
N	74	100	100	100	100	100	100	100	100	81	
M.. ..	20.7	22.3	22.8	24.9	25.9	19.1	20.4	21.4	22.8	23.6	
Min.	16.3	18.8	19.4	20.1	21.1	16.0	16.6	16.5	17.3	18.5	
Maks.	25.5	26.7	28.5	30.6	34.0	24.0	25.9	27.0	27.6	27.0	
s	1.79	1.97	1.94	2.07	2.19	1.51	1.79	1.90	1.98	1.56	
v	8.63	8.83	8.51	8.31	8.46	7.89	8.77	8.86	8.68	6.61	
±m	0.21	0.20	0.19	0.21	0.22	0.15	0.18	0.19	0.20	0.17	
% Toename ..	1.6 0.5 2.1 1.0					1.3 1.0 1.4 0.8					
	5.2 = 25.1%					4.5 = 23.6%					

Die gemiddelde omvang van die regterbo-arm van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 47).

Tabel 47

Verskil in die gemiddelde grootste omvang van die regterbo-arm van die ouderdomsgroepe

13	14	15	16	17
1.6	1.9	1.4	2.1	2.3

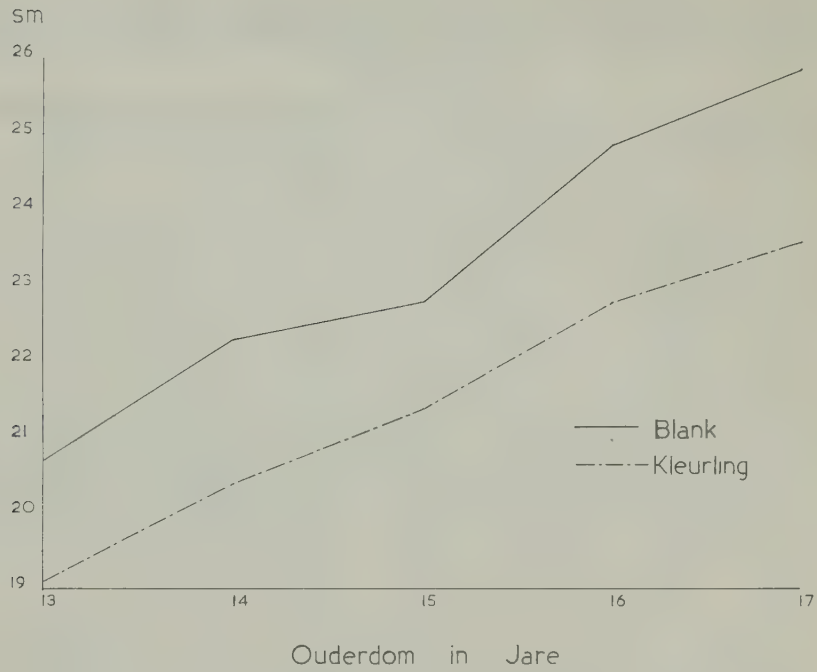
Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in bo-armomvang 5.2 sm. (25.1%) terwyl die toename by die Kleurlingseuns 4.5 sm. (23.6%) is (vgl. Tabel 46).

Die toename in bo-armomvang geskied meer reëlmatig by die Kleurlingseuns (vgl. Figuur 18).

Figuur 18

Grafiese voorstelling van die toename in omvang van die regterbo-arm



19(b) Grootste omvang van die regterbo-arm — gespan

Tabel 48

Gemiddelde grootste omvang van die regterbo-arm (gespan) van die ouderdomsgroepe

	Blank					Kleurling						
	Ouderdom in Jare											
	13	14	15	16	17	13	14	15	16	17		
N	74	100	100	100	100	100	100	100	100	81		
M.. .. .	23.2	25.1	26.0	28.1	29.8	21.4	23.0	24.4	25.9	27.0		
Min. .. .	18.3	21.1	21.8	21.8	24.0	18.0	18.3	18.7	19.2	21.0		
Maks. .. .	28.6	33.0	33.7	35.8	40.0	26.7	28.6	30.0	31.3	31.0		
s	1.87	2.37	2.30	2.54	2.61	1.71	2.15	2.31	2.68	1.95		
v	8.06	9.44	8.85	9.03	8.75	7.96	9.35	9.47	10.35	7.22		
±m	0.22	0.24	0.24	0.25	0.26	0.17	0.22	0.23	0.27	0.22		
% Toename ..	1.9 0.9 2.1 1.7					1.6 1.4 1.5 1.1						
	6.6 = 28.4%					5.6 = 26.2%						

Die gemiddelde omvang van die regterbo-arm — gespan, van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 49).

Tabel 49

Verskil in die gemiddelde grootste omvang van die regterbo-arm (gespan) van die ouderdomsgroepe

13	14	15	16	17
1.8	2.1	1.6	2.2	2.8

Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in dié omvang 6.6 sm. (28.4%) terwyl die toename by die Kleurlingseuns 5.6 sm. (26.6%) is (vgl. Tabel 48).

19(c) *Maksimale uitsetting van die bo-arm*

Die gemiddelde maksimale uitsetting van die blanke seuns is baie effens groter as dié van die Kleurlingseuns in elke ouderdomsgroep.

Tabel 50

Gemiddelde maksimale uitsetting van die bo-arm van die ouderdomsgroepe

Uitsetting van die regterbo-arm			
Jare	Blanke	Kleurling	Verskil
13	2.5	2.3	0.2
14	2.8	2.6	0.2
15	3.2	3.0	0.2
16	3.2	3.1	0.1
17	3.9	3.4	0.5

By albei groepe word die maksimale uitsetting van 13-17 jaar groter, met die maksimum uitsetting by 17 jaar.

Hierdie omvangmaat staan in die lig van spierontwikkeling en soos gesien kan word in Tabel 50 is die absolute verskille baie gering.

20 *Grootste omvang van die regtervoorarm*

Tabel 51

Gemiddelde grootste omvang (M) van die regtervoorarm van die verskillende ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	81	
M..	21·9	23·3	24·2	25·7	26·5	20·5	21·7	22·7	23·8	24·3	
Min.	19·2	21·1	21·0	22·0	23·0	18·0	18·3	18·6	19·6	20·3	
Maks.	24·6	27·2	29·0	30·2	30·9	24·5	25·7	26·4	26·8	27·0	
s	1·19	1·34	1·51	1·42	1·56	1·20	1·54	1·43	1·44	1·31	
v	5·43	5·75	6·24	5·53	5·89	5·87	7·10	6·30	6·05	5·39	
±m	0·14	0·13	0·15	0·14	0·16	0·12	0·15	0·14	0·14	0·15	
% Toename	1·4 0·9 1·5 0·8					1·2 1·0 1·1 0·5					
	4·6 = 21·0%					3·8 = 18·5%					

Die gemiddelde voorarmomvang van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 52).

Tabel 52

Verskil in die gemiddelde grootste omvang van die regtervoorarm van die verskillende ouderdomsgroepe

13	14	15	16	17
1.4	1.6	1.5	1.9	2.2

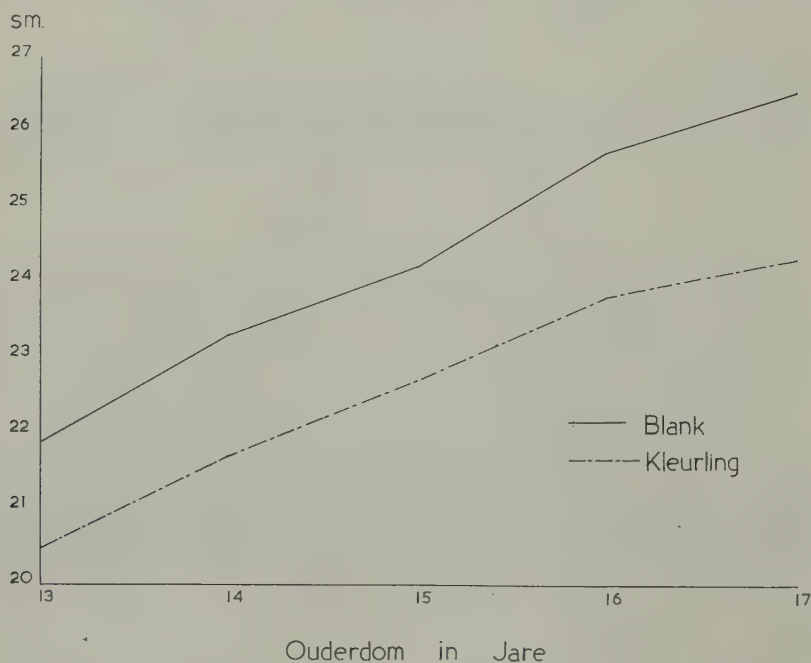
Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in voorarmomvang 4.6 sm. (21.0%) terwyl die toename by die Kleurlingseuns 3.8 sm. (18.5%) is (vgl. Tabel 51).

Die toename in voorarmomvang geskied meer reëlmatig by die Kleurlingseuns (vgl. Figuur 19).

Figuur 19

Grafiese voorstelling van die toename in die omvang van die regtervoor-arm



21 Grootste omvang van die regterdy

Tabel 53

Gemiddelde grootste omvang (M) van die regterdy van die verskillende ouderdomsgroepe

			Blank					Kleurling				
			Ouderdom in Jare									
			13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17
N	74	100	100	100	100	100	100	100	100	80
M.	44.4	46.9	47.7	50.6	53.1	40.6	42.5	45.0	46.6	48.5
Min.	36.8	39.9	40.0	42.0	40.7	33.5	36.5	37.3	38.0	39.8
Maks.	55.5	58.5	57.1	62.2	67.4	53.0	55.2	56.0	53.8	55.6
s	3.63	3.97	3.58	3.39	4.31	2.76	3.73	4.10	3.93	3.24
v	8.18	8.46	7.49	6.70	8.12	6.79	8.78	9.10	8.43	6.68
±m	0.42	0.40	0.36	0.34	0.43	0.28	0.37	0.41	0.39	0.36
% Toename	..		2.5	0.8	2.9	2.5		1.9	2.5	1.6	1.9	
			8.7 = 19.6%					7.9 = 19.5%				

Die gemiddelde omvang van die regterdy van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 54).

Tabel 54

Verskil in die gemiddelde grootste omvang van die regterdy van die verskillende ouderdomsgroepe

13	14	15	16	17
3.8	4.4	2.7	4.0	4.6

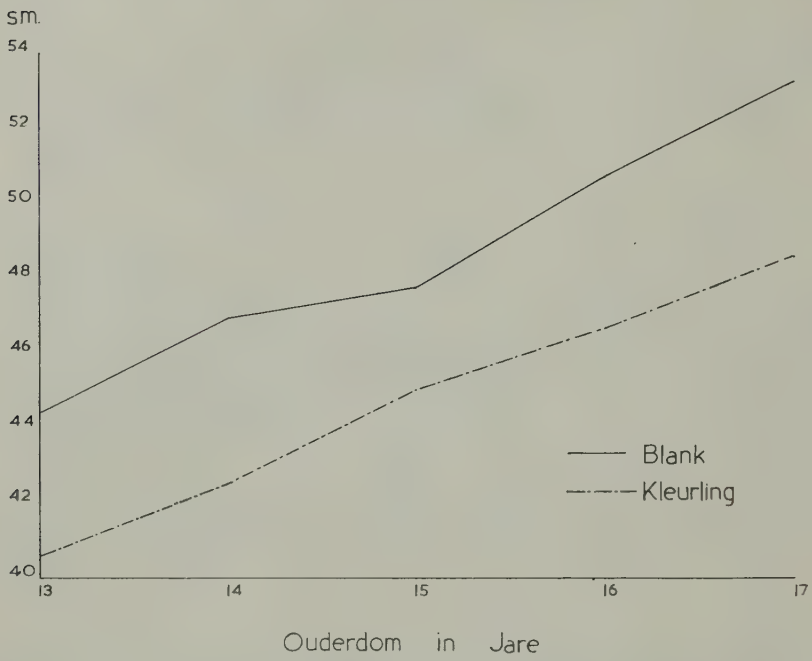
Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in dy-omvang 8.7 sm. (19.6%) terwyl die toename by die Kleurlingseuns 7.9 sm. (19.5%) is.

Die toename in dy-omvang geskied meer reëlmatig by die Kleurlingseuns (vgl. Figuur 20).

Figuur 20

Grafiese voorstelling van die toename in die omvang van die regterdy



22 Grootste omvang van die regterkuit

Tabel 55

Gemiddelde grootste omvang (M) van die regterkuit by die verskillende ouderdomsgroepe

			Blank					Kleurling				
			Ouderdom in Jare									
			13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17
N	74	100	100	100	100	100	100	100	100	81
M..	29.7	31.8	32.4	33.9	35.5	27.6	28.9	30.2	31.4	32.4
Min.	25.2	27.5	27.8	29.1	25.5	24.2	24.8	25.7	24.6	26.5
Maks.	38.2	37.4	39.3	38.3	46.2	35.5	34.2	35.5	36.3	37.0
s	2.24	2.23	2.58	1.90	2.77	1.90	2.24	2.16	2.08	1.97
v	8.18	7.01	7.96	5.62	7.80	6.89	7.75	7.15	6.62	6.08
±m	0.26	0.22	0.26	0.19	0.28	0.19	0.22	0.21	0.21	0.22
% Toename	..		2.1	0.6	1.5	1.6		1.3	1.3	1.2	1.0	
			5.8 = 19.5%					4.8 = 17.4%				

Die gemiddelde kuitomvang van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 56).

Tabel 56

Verskil in die gemiddelde kuitomvang van die verskillende ouderdomsgroepe

13	14	15	16	17
2.1	2.9	2.2	2.5	3.1

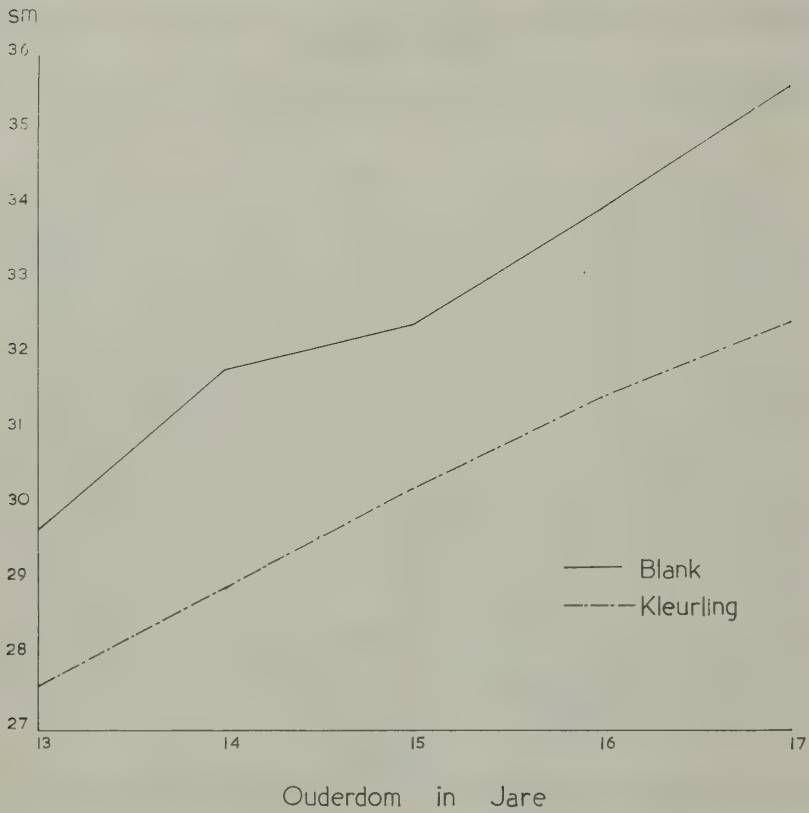
Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in kuitomvang 5.8 sm. (19.5%) terwyl die toename by die Kleurlingseuns 4.8 sm. (17.4%) is (vgl. Tabel 55).

Die toename in kuitomvang geskied meer reëlmatig by die Kleurlingseuns (vgl. Figuur 21).

Figuur 21

Grafiese voorstelling van die toename in die omvang van die regterkuit



23 Buikomvang

Tabel 57

Gemiddelde buikomvang (M) van die verskillende ouderdomsgroepe

				Blank					Kleurling						
				Ouderdom in Jare											
				13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•	
N		74	100	100	100	100		100	100	100	100	100	
M..		64·8	67·3	69·4	72·4	75·0		58·8	61·1	64·1	65·9	67·0	
Min.		51·0	61·0	60·3	63·5	64·9		52·5	53·0	54·5	56·0	56·2	
Maks.		79·0	89·5	89·5	88·8	104·5		76·0	74·0	81·0	74·2	75·5	
s	4·77	5·07	5·58	4·05	6·20		3·40	4·05	4·60	3·61	3·57	
v	7·36	7·53	8·04	5·59	8·27		5·77	6·63	7·18	5·48	5·33	
±m		0·55	0·51	0·56	0·41	0·62		0·34	0·41	0·46	0·36	0·40	
% Toename				..	2·5	2·1	3·0	2·6		2·3	3·0	1·8	1·1		
				10·2 = 15·7%					8·2 = 13·9%						

Die gemiddelde buikomvang van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 58).

Tabel 58

Verskil in die gemiddelde buikomvang van die verskillende ouderdomsgroepe

13	14	15	16	17
6.0	6.2	5.3	6.5	8.0

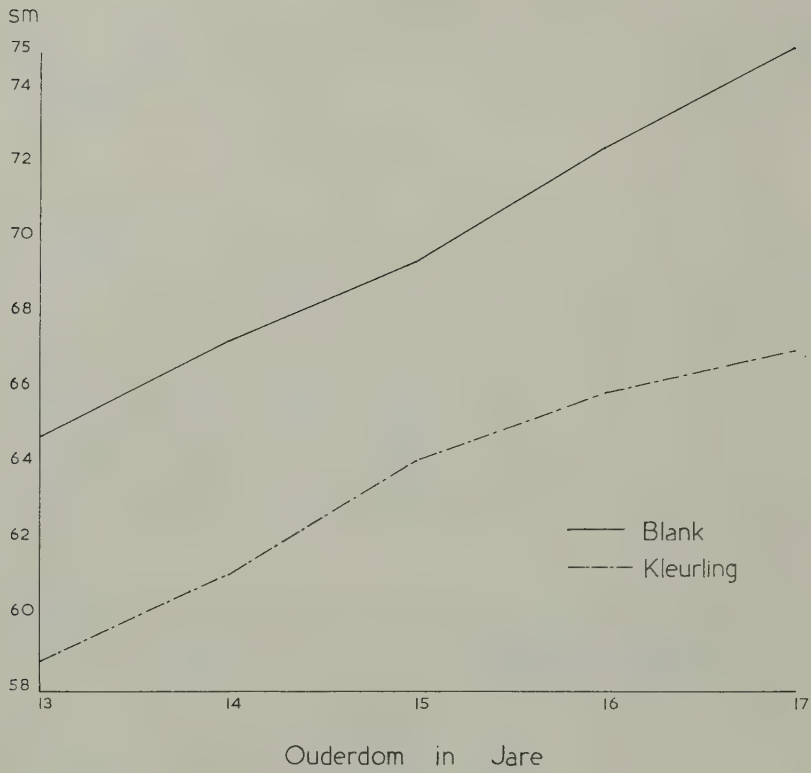
Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in buikomvang 10.2 sm. (15.7%) terwyl die toename by die Kleurlingseuns 8.2 sm. (13.9%) is (vgl. Tabel 57).

Die toename in buikomvang geskied effens meer reëlmatig by die blanke seuns (vgl. Figuur 22).

Figuur 22

Grafiese voorstelling van die toename in buikomvang



24 Gewig

Tabel 59

Gemiddelde gewig (M) van die verskillende ouderdomsgroepe

	Blank					Kleurling					
	Ouderdom in Jare										
	13	• 14	• 15	• 16	• 17	13	• 14	• 15	• 16	• 17	•
N	74	100	100	100	100	100	100	100	100	100	
M.. ..	92	108	118	135	146	76	87	99	110	119	
Min.	66	77	86	94	104	57	60	70	80	82	
Maks.	135	153	171	229	241	117	134	144	156	155	
s	13.50	16.30	18.28	21.4	18.73	11.03	15.3	15.33	14.81	14.28	
v	14.67	15.09	15.49	15.85	12.83	14.51	17.58	15.48	13.46	12.0	
m±	1.57	1.63	1.83	2.14	1.87	1.10	1.5	1.53	1.48	1.43	
% Toename ..	(16 10) (17 11)					(11 12) (11 9)					
	= 26 = 28					= 23 = 20					
	54 = 58.7%					43 = 56.6%					

Die blanke seuns weeg gemiddeld swaarder as die Kleurlingseuns in elke ouderdomsgroep. Die verskille is soos volg:

Tabel 60

Verskil in die gemiddelde gewig van die verskillende ouderdomsgroepe

13	14	15	16	17
16	21	19	25	27

Volgens die t-toets is al die verskille hoogs beduidend.

By die blanke seuns is die toename in gewig 54 pond (58.7%) terwyl die toename by die Kleurlingseuns 43 pond (56.6%) is (vgl. Tabel 59).

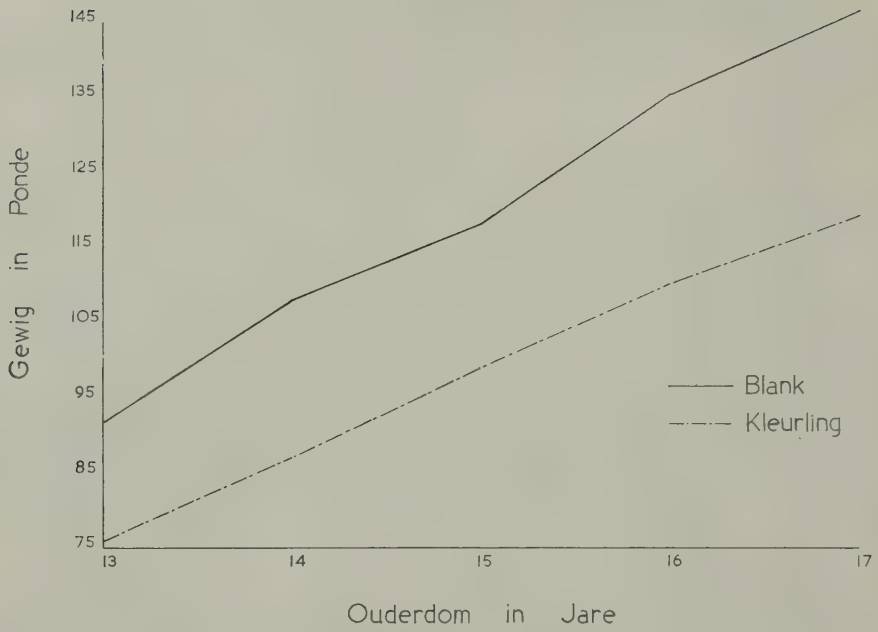
Die blanke seuns toon 'n toename van 26 pond van 13-15 jaar terwyl die toename by die Kleurlingseuns 23 pond is. Die toename vanaf 15-17 jaar is groter by die blanke seuns (28 pond) as by die Kleurlingseuns (20 pond).

Soos gesien in Tabel 59 is die standaardafwyking(s) groot by albei groepe in elke ouderdomsgroep. Verder is die standaardafwyking groter by die blanke seuns in elke ouderdomsgroep.

Die toename in gewig geskied meer reëlmatig by die Kleurlingseuns (vgl. Figuur 23).

Figuur 23

Grafiese voorstelling van die toename in gewig



25 *Grootste lengte van die kop*

Tabel 61

Gemiddelde koplengte (M) van die verskillende ouderdomsgroepe

				Blank					Kleurling																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																			
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Die gemiddelde koplengte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 62).

Tabel 62

Verskil in die gemiddelde maksimum koplengte van die verskillende ouderdomsgroepe

13	14	15	16	17
0.2	0.4	0.4	0.3	0.2

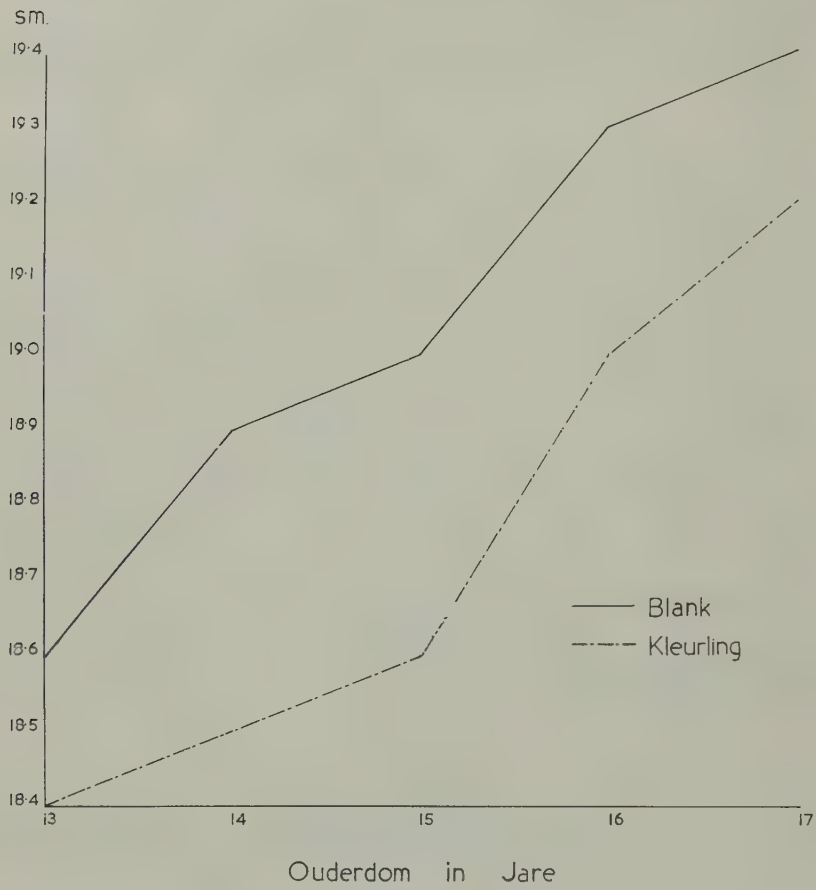
Volgens die t-toets is al die verskille hoogs beduidend by die 1%-grens in die ouderdomsgroepe 14, 15 en 16 jaar. Die verskille in die ouderdomsgroepe 13 en 17 jaar is beduidend by die 5%-grens.

Die toename in koplengte is by albei groepe dieselfde (vgl. Tabel 61).

Die toename in koplengte is taamlik onreëlmatig by die blanke seuns sowel as by die Kleurlingseuns (sien figuur 24).

Figuur 24

Grafiese voorstelling van die toename in die lengte van die kop



26 Grootste breedte van die kop

Tabel 63

Gemiddelde grootste kopbreedte (M) van die verskillende ouderdomsgroepe

	Blank					Kleurling				
	Ouderdom in Jare									
	13	14	15	16	17	13	14	15	16	17
N	74	100	100	100	100	100	100	100	100	91
M.. .. .	14·6	14·8	14·9	15·0	15·0	14·3	14·4	14·5	14·6	14·7
Min. .. .	13·8	13·9	13·9	13·9	13·8	13·3	13·4	13·5	13·4	13·5
Maks. .. .	15·8	15·8	16·3	16·2	16·2	15·9	15·8	15·7	15·7	16·3
s	0·44	0·36	0·52	0·50	0·43	0·46	0·45	0·49	0·49	0·48
v	2·98	1·44	3·49	3·33	2·87	3·23	3·10	3·38	3·32	3·29
±m	0·05	0·04	0·05	0·05	0·04	0·05	0·05	0·05	0·05	0·05
% Toename ..	0·2 0·4 = 2·74%					0·1 0·4 = 2·80%				

Die gemiddelde kopbreedte van die blanke seuns is groter in elke ouderdomsgroep (vgl. Tabel 64).

Tabel 64

Verskil in die gemiddelde kopbreedte van die verskillende ouderdomsgroepe

13	14	15	16	17
0.3	0.4	0.4	0.4	0.3

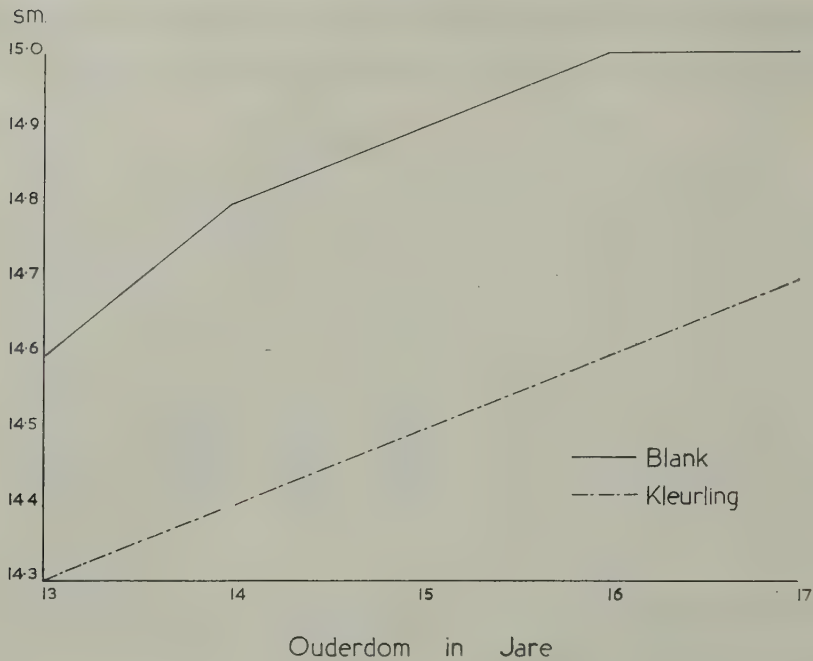
Volgens die t-toets is al die verskille hoogs beduidend.

Die toename in kopbreedte is by albei groepe dieselfde (vgl. Tabel 63).

Die toename in kopbreedte geskied reëlmatig by die Kleurlingseuns in teenstelling met die toename by die blanke seuns (vgl. Figuur 25).

Figuur 25

Grafiese voorstelling van die toename in kopbreedte



27 *Korrelasie van liggaamslengte, gewig en ouderdom van blanke en Kleurlingseuns van 13 tot 17 jaar.*

Die gemiddelde gewig van die blanke seuns van 13—17 jaar is oorewegend groter as dié van die Kleurlingseuns vir 'n gegewe lengte (vgl. Tabel 65). Hierdie verskil in gewig word groter met die styging van die liggaamslengte groter as 166.0 sm.

Liggaamslengte in sm.	OUDERDOM IN JARE												Gemiddelde Gewig		
	13			14		15		16		17					
	B.	K.	B.	K.	B.	K.	B.	K.	B.	K.					
130		60.3 (3)		63.7 (3)								B.	K.	B.	K.
133		66.4 (7)		68.0 (1)											
136		66.7 (15)		67.0 (4)											
139	73.3 (3)	72.3 (27)	78.0 (1)	72.3 (11)			65.0 (1)							75.7 (4)	69.9 (39)
142	76.0 (2)	76.9 (12)	83.0 (1)	77.8 (9)			78.2 (6)							79.5 (3)	77.6 (27)
145	83.2 (12)	77.1 (15)	84.0 (5)	77.7 (15)			87.0 (9)		84.3 (4)					83.6 (17)	81.5 (43)
148	88.5 (15)	85.2 (6)	99.4 (9)	85.9 (16)	90.0 (1)		87.9 (12)		82.8 (5)					92.6 (25)	85.5 (39)
151	87.9 (9)	95.4 (5)	95.5 (13)	89.5 (12)	96.3 (7)		94.1 (11)		99.3 (9)					93.2 (29)	93.4 (39)
154	92.3 (12)	95.3 (4)	101.9 (9)	97.8 (8)	99.3 (6)		94.5 (17)		101.8 (4)					97.8 (27)	98.1 (35)
157	103.3 (9)	94.0 (1)	108.2 (20)	98.5 (13)	105.9 (12)		101.6 (10)		97.2 (16)	125.7 (3)				109.2 (50)	99.8 (50)
160	106.8 (6)	110.0 (2)	108.9 (9)	110.4 (7)	103.6 (9)		110.5 (14)		110.0 (11)	115.5 (2)				110.0 (30)	110.4 (49)
163	110.0 (6)		114.2 (9)	105.5 (2)	111.3 (12)		114.2 (12)		116.3 (24)	122.0 (4)				116.6 (39)	113.9 (60)
166			114.7 (7)		123.4 (16)		121.0 (2)		118.6 (12)	119.0 (8)				120.8 (50)	120.1 (33)
169			118.5 (8)	122.0 (3)	125.2 (11)		115.8 (4)		130.2 (5)	137.4 (21)				128.1 (53)	122.7 (24)
172			134.8 (5)		130.9 (8)		117.0 (1)		118.6 (7)	146.5 (17)				137.2 (48)	123.9 (17)
175			137.3 (4)		135.7 (7)		140.0 (1)		121.5 (2)	147.3 (13)				139.9 (42)	133.4 (6)
178					138.7 (6)				137.0 (1)	156.1 (12)				147.7 (29)	139.5 (3)
181					148.5 (2)					156.2 (12)				169.1 (16)	153.0 (1)
184					144.0 (1)					188.0 (7)				158.7 (9)	
187					171.0 (1)					167.0 (1)				169.0 (2)	

B INDEKSE

1 *Liggaamsmate relatief tot liggaamslengte*

Tabel 66

Liggaamsmate as persentasies van die liggaamslengte in die verskillende ouderdomsgroepe

Liggaamsmaat	Blank					Kleurling				
						Ouderdom in Jare				
	13	14	15	16	17	13	14	15	16	17
Suprasternale hoogte	81·2	81·3	81·7	81·3	81·6	80·4	81·7	81·9	82·0	81·9
Akromiale hoogte	81·1	81·1	81·8	81·4	81·7	81·3	81·7	81·7	81·8	81·4
Nawelhoogte	60·7	60·7	60·9	60·7	60·6	60·3	60·5	60·8	60·8	60·6
Symphysionhoogte	52·8	52·9	52·7	53·0	52·8	52·3	52·3	52·6	52·7	52·5
Iliospinale hoogte	56·4	56·5	56·7	56·3	55·9	56·4	56·0	56·3	56·4	56·1
Voorste Romplengte	28·3	28·3	28·3	28·2	28·7	29·1	29·3	29·3	29·4	29·3
Sithoogte	51·2	51·4	51·4	51·5	52·1	51·6	51·3	51·2	51·1	51·1
Spanwydte	102·4	103·1	104·2	103·6	104·3	104·2	104·2	104·9	105·2	105·6
Beenlengte	54·9	55·1	55·3	55·1	54·8	54·7	54·7	54·9	54·8	54·6
Armlengte	43·8	44·3	44·7	44·5	44·9	44·4	45·1	45·0	45·2	44·8
Buikomvang	42·4	42·2	41·7	42·4	42·9	41·1	40·7	41·0	40·6	40·4

Van die ouderdom 13—17 jaar is dit opvallend dat die Kleurlingseuns 'n relatiewe langer voorste romplengte het as die blanke seuns. Daarenteen is die relatiewe buikomvang van die Kleurlingseuns kleiner as dié van die blanke seuns.

Die relatiewe spanwydte is groter by die Kleurlingseuns en neem van 13—17 jaar toe in verhouding met die liggaamslengte. Laasgenoemde verandering is ook by die blanke seuns te sien.

Die relatiewe suprasternale hoogte, akromiale hoogte, nawelhoogte, symphysionhoogte, iliospinale hoogte, sithoogte, beenlengte en armlengte van die blanke seuns verskil in 'n geringe mate van dié van die Kleurlingseuns. Geen opvallende verandering tree in dié indekse van 13—17 jaar op nie.

2 Liggaamsmate relatief tot voorste romplengte

Tabel 67

Liggaamsmate as persentasies van die voorste romplengte in die verskillende ouderdomsgroepe

Liggaamsmaat	Blank					Kleurling				
	Ouderdom in Jare									
	13	14	15	16	17	13	14	15	16	17
Armlengte	154·7	156·4	157·0	157·6	156·3	152·9	153·9	153·8	153·7	153·2
Beenlengte	194·0	194·7	194·1	195·0	191·0	188·2	186·4	187·4	186·6	186·8
Mammillare breedte	38·6	38·3	38·6	40·3	40·5	38·5	37·3	38·5	38·4	38·4
Iliospinale breedte	45·9	44·7	46·2	45·5	45·5	42·8	41·8	42·7	41·7	41·7
Bekkenbreedte	55·9	55·8	55·5	55·9	55·7	52·4	52·5	52·7	52·6	52·4

Die relatiewe armlengte van die blanke seuns is groter as by die Kleurlingseuns van 13—17 jaar. Geen opvallende verandering in dié indeks kom voor van 13—17 jaar by albei groepe nie.

Die relatiewe beenlengte van die blanke seuns is groter as by die Kleurlingseuns. Geen opvallende verandering kom voor van 13—17 jaar by albei groepe nie.

Die relatiewe mammillare breedte verskil baie min by albei groepe.

Die relatiewe iliospinale breedte asook die relatiewe bekkenbreedte is groter by die blanke seuns.

3 Bykomende indekse

Tabel 68

Indeks				Blank					Kleurling				
				Ouderdom in Jare									
				13	14	15	16	17	13	14	15	16	17
Armlengte	$\times \frac{100}{\text{Beenlengte}}$	79.8	80.3	80.9	80.8	81.8	81.2	82.6	82.0	82.4	82.0
Iliospinale breedte	$\times \frac{100}{\text{Bekkenbreedte}}$	82.2	80.2	83.3	81.2	81.7	81.6	79.7	80.6	79.3	79.5
Bekkenbreedte	$\times \frac{100}{\text{Skouerbreedte}}$	72.7	72.2	72.7	71.7	71.0	68.8	69.4	69.1	68.6	67.5
Voorarmomv.	$\times \frac{100}{\text{Bo-armomv.}}$	105.8	104.5	106.1	103.2	102.3	107.4	106.4	106.0	104.4	103.0
Kuitomvang	$\times \frac{100}{\text{Dyomvang}}$	66.9	67.8	67.9	67.0	66.9	68.0	68.0	67.1	67.4	66.8
Borsdiepte	$\times \frac{100}{\text{Borsbreedte}}$	72.6	73.6	71.7	73.7	73.3	69.2	69.3	68.6	68.8	68.4

Dit is opvallend dat die voorarmomvang relatief tot die bo-armomvang by albei groepe van 13—17 jaar kleiner word.

4 Kopindeks

Tabel 69

Kopindeks	Blank					Kleurling				
	Ouderdom in Jare									
	13	14	15	16	17	13	14	15	16	17
$\frac{\text{Breedte van kop}}{\text{Lengte van kop}} \times \frac{100}{1}$	78.5	78.3	78.4	77.7	77.3	77.7	77.8	77.9	76.8	76.6

Die verskil in dié indeks is gering by albei groepe van 13—17 jaar. Volgens die klassifikasie van Martin (1928) is albei groepe van 13—17 jaar oorwegend mesokefaal.

C 'N VERGELYKING VAN DIE GEMIDDELDE LIGGAAMSMATE VAN 17-JARIGE KLEURLINGSEUNS EN VOLWASSE KAAPSE KLEURLINGE

In vergelyking met die resultate van Van Wyk (1939), waar die gemiddelde liggaamsmate van volwasse Kleurlinge aangegee word, is die lengteas-mate van die volwasse Kleurlinge *minder* as dié van die 17-jarige Kleurlingseuns. Die breedtemate sowel as die omvangmate is egter groter by eersgenoemde groep.

Tabel 70

Liggaamsmate van volwasse Kleurlinge (Van Wyk) en 17-jarige Kleurlingseuns

Liggaamsmaat	Volwasse Kleurlinge	17-jarige Kleurlingseuns
Liggaamslengte	162.2	165.8
Suprasternale hoogte	133.2	135.7
Akromiale hoogte	132.7	134.9
Nawelhoogte	97.3	100.5
Symphysionhoogte	84.9	87.1
Iliospinale hoogte	90.5	93.0
Spanwydte	170.9	175.2
Sithoogte	82.5	84.8
Romplengte	48.3	48.5
Armlengte	73.4	74.3
Beenlengte	88.5	90.6
Skouerbreedte	38.0	37.6
Bekkenbreedte	26.2	25.4
Iliospinale breedte.. .. .	21.0	20.2
Borsomvang, norm., rust. res.	87.0	81.2
„ inspirasie	89.3	84.6
„ ekspirasie	84.1	79.1
Bo-armomvang	25.8	23.6
Bo-armomvang gespan	29.1	27.0
Voorarmomvang	25.6	24.3
Dyomvang	47.7	48.5
Kuitomvang	32.0	32.4
Koplengte	191.0	192.0
Kopbreedte	147.0	147.0

Volgens Fischer (1913), is die gemiddelde lengte van die volwasse Rhehoboth-basters 168.4 sm., 'n lengte wat reeds by 17/18 jarige leeftyd bereik word. Die verklaring vir die verskil in die gemiddelde liggaamslengte van die 17-jarige Kleurlingseuns (165.8 sm.) en volwasse Kleurlinge (162.2 sm.) (Van Wyk, 1939), lê heelwaarskynlik daarin dat die genetiese oorsprong van die volwasse Kleurlinge (Van Wyk, 1939) nie dieselfde as dié van die Kleurlingseuns is nie. 'n Ander faktor wat in aanmerking geneem moet word, is die voeding. Dit is ongetwyfeld seker dat die voedingspeil van die Kleurlingseuns van vandag hoër is of beter vergelyk met dié van die volwasse Kleurlinge toe hulle seuns was.

V PUBERTEIT

Die woord „puberteit” verwys primêr na die skaambeharing op die pubis. In breër sin verwys dit na die hele proses van geslagsrypwording. Hierdie proses kan van 2 tot 4 jaar, of langer, duur (Zuckerman, 1956). Die aanvang van puberteit by die seuns word aangedui deur die verskyning van die terminale- of skaambeharing op die pubis. Kinsey, et. al. (1948) beweer dat hierdie stelling vir 85% van alle gevalle geld. Volgens Weissenberg (1911), Matthias (1916), Arnold (1931) en Zuckerman (1956) word die puberteitsperiode gekenmerk deur 'n fase van vinnige liggaamsgroei en 'n toename in die tempo van liggaamsontwikkeling in vergelyking met dié van die prepuberale fase of bi-seksuele kindheid. Hierdie vinnige groei word volgehou dwarsdeur die puberteitsjare en word verder voortgesit, alhoewel nie in dieselfde mate nie, in die adolessente jare (Zuckerman, 1956).

Uit my resultate blyk dit dat puberteit by die blanke seuns blykbaar vroeër begin as by die Kleurlingseuns.

Die persentasie seuns, blank en Kleurling, tussen 13—17 jaar by wie die terminale hare voorkom, word in tabel 71 met mekaar vergelyk.

Tabel 71

Voorkoms van terminale hare by die verskillende ouderdomsgroepe

Ouderdom in jare	Blanke	Kleurling
13	69%	55%
14	94%	61%
15	99%	92%
16	100%	99%
17	100%	100%

Matthias (1916) klassifiseer die puberteitsperiode aangaande die liggaamsontwikkeling in twee afdelings, nl.

- „Pubertätslangenwachstum” 12/13—16 jaar, met die maksimum lengtegroei by 14 en 15 jaar.
- „Pubertätsbreitenwachstum” 12/13—18 jaar, met die maksimum toename in omvang en breedtes by 16 en 17 jaar.

By die blanke seuns word die reëlmatige, snelle toename in lengte volgehou tot by 15 jaar. Vanaf 15—16 jaar neem die snelheid van toename in

lengtegroei af en neem verder af van 16—17 jaar. In ooreenstemming met die bevinding van Matthias, blyk die maksimum lengte-toename by 14/15 jaar te wees by die blanke seuns wat ek ondersoek het.

Die periode van maksimale lengte-toename begin by die Kleurlingseuns, net soos by die blanke seuns, by ± 14 jaar maar word nog volgehou tot by 16 jaar.

Bogenoemde waarnemings is in ooreenstemming met die algemene stelling van Tanner (1955) aangaande die puberteitsgroei. Tanner maak die volgende stelling:

„ . . there is marked acceleration of growth which is known as the adolescent growth spurt. The adolescent spurt is a constant phenomenon and occurs in all children, though it varies in intensity and duration from one child to another. In boys it takes place, on the average, from age 13 to 15½, and is responsible for a gain in height of about 8 inches (range 4—12 inches) accompanied by a gain in weight of about 40 lb. (range 15—65 lb.). The peak velocity of height growth averages about 4 inches (10 cm.) per year, which is the rate the boy was growing at age 2. The time at which this maximum velocity is reached averages about 14 years, though it may lie anywhere between 12 and 17.”

Die toename in omvangmate en liggaamsbreedtes bereik die maksimum by 14/16 jaar by die blanke seuns terwyl in die geval van die Kleurlingseuns die maksimum by 15/16 jaar bereik word en dan afneem.

In die lig gesien van hierdie groeiverskille tussen die twee groepe tesame met die waarneming van die vroeëre verskyning van die pubis-beharing by die blanke seuns, staan hierdie verskille heelwaarskynlik in die teken van die vroeëre aanvang van puberteit by die blanke seuns.

VI BESPREKING

Die seuns wat in aanmerking geneem is in hierdie ondersoek was almal fisies normale kinders. Die 974 seuns wie se liggaamsmate gebruik was om die rekenkundige gemiddeldes te bepaal, moet beskou word as verteenwoordigend vir seuns woonagtig in dié streek waaruit die monster geneem is.

Alhoewel ek in hierdie ondersoek geen pogings gemaak het om die seuns te klassifiseer in verskillende liggaamsbou-tipes volgens die klassieke indeling van Sheldon (1940) nie, nl. endomorfies (gerond en vet), mesomorfies (muskulêr) en ektomorfies (lenig), was die seuns hoofsaaklik van die mesomorfe (komponent II) en ektomorfe (komponent III) tipes. 'n Klein persentasie was van die endomorfe (Komponent I) tipe, alhoewel uitermatig vet seuns uitgeskakel is.

Soos gesien in die rekenkundige gemiddeldes vir die verskillende liggaamsmate, Tabele 5—65, is die blanke seuns groter in liggaamsbou as die Kleurlingseuns en die verskille in grootte is almal van 'n betekenisvolle aard (t-toets vir beduidendheid van verskille).

Die liggaamslengte van die blanke seuns en Kleurlingseuns word in tabel 72 in vergelyking gebring met ander Suid-Afrikaanse gegewens asook dié van seuns gemeet in Kanada en Engeland.

Tabel 72

Bevolkingsgroep	13	14	15	16	17	Outeur
Blanke seuns	152·9	159·6	166·4	171·4	174·5	Outeur
Kleurlingseuns	143·1	150·0	156·2	162·3	165·8	Outeur
Rehobother basterseuns ..	144·4	143·2	151·6	163·2	168·4	Fischer (1913)
Suid-Afrikaanse seuns ..	150·9	158·1	164·4	169·4	—	Postma (1950)
Suid-Afrikaanse seuns ..	152·5	158·9	165·8	170·7	174·3	Grobbelaar*
Kanadese seuns	150·6	158·0	164·3	169·4	(16-17)	le Riche (1953)
Engelse seuns	152·1	159·0	165·4	169·9	173·7	Clements en Pickett (1953)†

* Nog in voorbereiding

† Aangehaal deur Zuckerman (1956)

Die liggaamsgewig van die blanke seuns en Kleurlingseuns word in tabel 73 met dieselfde materiaal vergelyk.

Tabel 73

Bevolkingsgroep	13	14	15	16	17	Outeur
Blanke seuns	92	108	118	135	146	Outeur
Kleurlingseuns	76	87	99	110	119	Outeur
Suid-Afrikaanse seuns ..	89	99	115	125	—	Postma (1950)
Suid-Afrikaanse seuns ..	93	105	119	133	144	Grobbelaar*
Kanadese seuns	94	108	119	136	(16-17)	le Riche (1953)
Engelse seuns	93	105	116	129	137	Clements en Pickett (1953)†

* Nog in voorbereiding

† Aangehaal deur Zuckerman (1956)

Uit meegaande tabelle (72 en 73), blyk dit dat die Kleurlingseuns korter is en minder weeg as enige ander genoemde groep in elke ouderdomsgroep van 13—17 jaar.

Die vergelyking van die groeibeeld soos gesien in die verskillende lengte-as-mate kan as volg saamgevat word:

- 1 Die absolute sowel as die persentuele toename in liggaamslengte van 13—17 jaar is groter by die Kleurlingseuns as by die blanke seuns. Dieselfde geld vir die ander lengte-as-mate nl. die hoogte van die suprasternale,

hoogte van die nawel, hoogte van die symhysion, hoogte van die regter-iliospinale, hoogte van die regter-akromion, spanwydte van die arms, lengte van die regterbeen en die voorste romplengte.

- 2 Daarenteen is die absolute en persentuele toename in sithoogte groter by die blanke seuns as by die Kleurlingseuns.
- 3 Die absolute toename in die lengte van die regterarm is groter by die blanke seuns maar die persentuele toename is min of meer dieselfde by die twee groepe.
- 4 By al die lengteas-mate, uitgesonderd sithoogte, is die absolute toename in liggaamsgroei by die blanke seuns van 13—15 jaar groter as dié van die Kleurlingseuns, terwyl die absolute toename by die Kleurlingseuns van 15—17 jaar groter is as dié van die blanke seuns.
- 5 Die toename in sithoogte van 13—15 jaar en van 15—17 jaar is groter by die blanke seuns as by die Kleurlingseuns.
- 6 By die blanke seuns begin die toename van al die lengteas-mate na die 15de jaar afneem en neem verdar af ná die 16de jaar. By die Kleurlingseuns tree hierdie afname deurgaans eers op na die 16de jaar (vgl. Figure 1—11). Die snelle puberteitsgroei eindig dus vroeër by die blanke seuns as by die Kleurlingseuns.

Die vergelyking van die groeibeeld soos gesien in die verskillende breedte-mate:

- 1 Die blanke seuns toon 'n groter absolute toename in skouerbreedte van 13—17 jaar as die Kleurlingseuns maar die persentuele toename is groter by die Kleurlingseuns.
- 2 Die absolute toename in bekkenbreedte is by albei groepe gelyk maar die persentuele toename is groter by die Kleurlingseuns.
- 3 Die absolute sowel as die persentuele toename in borsdiepte is groter by die blanke seuns.
- 4 Die absolute sowel as persentuele toename in mammillare breedte, ilio-spinale breedte en borsbreedte is groter by die blanke seuns.
- 5 Die toename in skouerbreedte, bekkenbreedte en borsdiepte is taamlik reëlmatig by albei groepe.
- 6 Die toename in mammillare breedte, iliospaneel breedte en borsbreedte is meer reëlmatig by die Kleurlingseuns as by die blanke seuns.

Die vergelyking van die groeibeeld van 13—17 jaar soos gesien in die verskillende omvang-mate:

- 1 Die absolute en persentuele toename in die borsomvang, omvang van die regter-boarm, omvang van die regter-voorarm, omvang van die regterdy, kuitomvang en buikomvang is by die blanke seuns groter as dié van die Kleurlingseuns.
- 2 Die toename in omvangmate van 13—17 jaar is meer reëlmatig by die Kleurlingseuns.

Die vergelyking van die groeibeeld van 13—17 jaar soos gesien in die kopmate:

- 1 Die toename in die koplengte is onreëlmatig by albei groepe.
- 2 Die toename in kopbreedte is reëlmatig by die Kleurlingseuns, onreëlmatig by die blanke seuns.

Die toename in liggaamsgewig van 13—17 jaar is by albei groepe reëlmatig. Die blanke seuns toon 'n groter variasie (standaardafwyking) in liggaamsgewig binne elke ouderdomsgroep as die Kleurlingseuns.

Soos reeds genoem, word die puberteitsperiode gekenmerk deur 'n fase van vinnige liggaamsgroei in vergelyking met dié van die prepuberale fase. By die blanke seuns hou hierdie snelle groei, die duidelikste gesien in die lengtegroei, reëlmatig aan tot by die 15-jarige leeftyd. By die Kleurlingseuns begin die snelle reëlmatige groei eers afneem na die 16-jarige leeftyd. Die Kleurlingseuns hou dus langer aan met groei.

Bogenoemde verskil in die liggaamsgroei en die verskyning van die vroeëre aanvang van die pubis-beharing, dui op 'n vroeëre aanvang van puberteit by die blanke seuns.

Die liggaamsverhoudings by blanke sowel as by Kleurlingseuns bly dieselfde van 13—17 jaar, soos gesien in die berekende indekse. Die liggaamsgroei as 'n geheel vind dus harmonies plaas. By die verskillende ouderdomsgroepe is die verskille in liggaamsverhoudinge by die blanke en Kleurlingseuns gering.

Die statistiese ontleding van elke reeks liggaamsmate het oor die algemeen betreklike klein standaardafwykings getoon by albei groepe. Die standaardafwykings, soos bereken vir die Kleurlingmate is in sekere gevalle gelyk en soms selfs kleiner as dié van die blanke seuns. Statisties gesproke dui hierdie klein standaardafwykings op 'n betreklike homogene monster materiaal. By die Kleurlingseuns, die meer heterogene bevolkingsgroep, kry ons 'n neiging tot homogeniteit, 'n kenmerk wat ook deur Van Wyk (1939) en Keen (1949) genoem word vir sekere fisiese kenmerke van volwasse Kleurlinge.

VII OPSOMMING

- 1 Die seuns gemeet was blanke en Kleurlingseuns in die skole in die Westelike Provinsie onder die Departement van Openbare Onderwys van die Kaapprovinsie.
- 2 474 Blanke en 500 Kleurlingseuns, tussen die ouderdomme 13—17 jaar, was volgens 'n gestandaardiseerde metode gemeet. 29 Liggaamsmate is by elke individu gemeet en 22 indekse bereken by elke ouderdomsgroep.
- 3 Die seuns van albei bevolkingsgroepe is elk in die 5 ouderdomsgroepe, 13—17 jaar, geklassifiseer. Die gegewens van elke liggaamsmaat, insluitende die grootste en kleinste maat, die rekenkundige gemiddelde, die standaardfout van die gemiddelde, standaardafwyking en die variasie koëffisiënt word in tabelvorm aangegee.
- 4 Die groeibeeld van die blanke en Kleurlingseuns, soos gesien in die gemiddelde mate, is bespreek met spesiale aandag aan die verskille in absolute en persentuele toename.
- 5 Betreffende al die liggaamsmate is die blanke seuns groter in liggaamsbou as die Kleurlingseuns.
- 6 Gebruikmakende van die t-toets is gevind dat al die verskille werklike verskille is.
- 7 Die gemiddelde lengte en gewig van die blanke en Kleurlingseuns is verge-

lyk met Suid-Afrikaanse, Kanadese en Engelse gegewens. Die Kleurlingseuns toon die kleinste liggaamslengte en gewig, van 13—17 jaar, in dié vergelyking.

- 8 Die gevolgtrekking word gemaak dat puberteit blykbaar vroeër in aanvang kom by die blanke seuns en ook gouer afgesluit raak as by die Kleurlingseuns.
- 9 Die homogeniteit van die Kleurlingseuns word in hierdie ondersoek bevestig.

SUMMARY

- 1 European and Cape Coloured school boys attending schools in the Western Province were chosen at random for measurement.
- 2 A total of 474 European and 500 Coloured boys, between the ages 13—17 years, were somatometrically measured according to the standardized method. On each subject 29 absolute measurements were taken and 22 indices were calculated for each age group.
- 3 The measurements of the boys, European and Coloured, were classified in the 5 age groups, 13—17 years.
The statistical analysis of each measurement is given in tabular form for comparison.
- 4 The growth pattern of the European and Coloured boys, as derived from the mean measurements, is discussed with special reference to the difference in absolute and percentual increase in growth.
- 5 The European boys are on the average taller than the Cape Coloured boys, as seen in *all* the average measurements.
- 6 The above mentioned differences proved to be statistically significant in all cases.
- 7 The average lengths and weights of the European and Coloured boys is compared with South African, Canadian and English data. The Coloured boys from 13—17 years are shorter in stature and they weigh less than any of the groups with which they have been compared.
- 8 The conclusion is drawn that the onset of puberty starts earlier and reaches its termination sooner in the case of European boys.
- 9 The homogeneity of the Cape Coloured boys, as seen in their physical characteristics, is undoubtedly apparent in this investigation.

VIII ERKENNING

Hiermee wil ek my opregte dank en erkenning uitspreek teenoor Dr. C. S. Grobbelaar vir sy waardevolle advies, kritiek en aktiewe belangstelling in verband met hierdie ondersoek. Ook word hy bedank vir die verlof toegestaan tot gebruikmaking van mate van blanke seuns deur homself versamel asook sy medewerking met die meet van blanke seuns.

Die W.N.N.R. word bedank vir die beurs-toekenning toegestaan aan hierdie ondersoek.

Mej. L. le Roux van die Departemente Anatomie en Fisiologie, Universiteit Stellenbosch, word hartlik bedank vir die tik van hierdie skripsie.

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No.		OUDERDOMS- GROEP:		PLEK EN DATUM VAN WAARNEMING:		WAARNEMER:				INDEX CEPH.	INDEKS R.L./L.L.	INDEKS ILIOSP. br./R.L.	INDEKS BEK./R.L.	INDEKS MAM./R.L.
VOORNAME:										$\frac{28 \times 100}{29}$	$\frac{27 \times 100}{1}$	$\frac{13 \times 100}{27}$	$\frac{12 \times 100}{27}$	$\frac{11 \times 100}{27}$
FAMILIENAAM:						PUBERTEIT:				INDEKS REL. hg. v. SUPPRAST.	INDEKS REL. hg. v. NAWEL	INDEKS REL. hg. v. SYMPH.	INDEKS REL. hg. ILIOSP.	INDEKS REL. ARM LENGTE
GESLAG:		RAS:				LATENT AANVANG PROMINENT				$\frac{2 \times 100}{1}$	$\frac{3 \times 100}{1}$	$\frac{4 \times 100}{1}$	$\frac{5 \times 100}{1}$	$\frac{26 \times 100}{1}$
OUDERDOM:		GEBORTEPLEK:												
LENGTE v	SUPPRAST. b. v.	NAWEL b. v.	SYMPH. b. v.	ILIOSP. b. v.	AKROM. b. v.	DARTY. b. v.	SPAN- WIDTE	SIT- HOOGTE	SKOUER- BREEDTE	INDEKS REL. BEEN- LENGTE	INDEKS ARM/R.L.	INDEKS ARM/BEEN	INDEKS BEEN/R.L.	INDEKS BEKKEN- BREEDTE
1	2	3	4	5	6	7	8	9	10	$\frac{25 \times 100}{1}$	$\frac{26 \times 100}{27}$	$\frac{26 \times 100}{25}$	$\frac{25 \times 100}{27}$	$\frac{13 \times 100}{12}$
MAMM.- BREEDTE	BEKKEN- GREEDTE	ILIOSP.- BREEDTE	BORS: NORMAAL	BORS: INSP.	BORS: EKSP.	BORS: TRANS.	BORS: SAG.	BO-ARM: GESTREK	BO-ARM: GESPAN	INDEKS ROMP- BREEDTE	INDEKS REL. SITHgt.	INDEKS REL. SPANW.	INDEKS V. ARM/B. ARM OMVANG	INDEKS KUIT/DY- OMVANG
11	12	13	14	15	16	17	18	19	20	$\frac{12 \times 100}{10}$	$\frac{9 \times 100}{1}$	$\frac{8 \times 100}{1}$	$\frac{21 \times 100}{19}$	$\frac{23 \times 100}{22}$
VOOR ARM OMV	DY- OMVANG	KUIT- OMVANG	BUIK- OMVANG	L. v. R. BEEN	L. v. R. ARM	L. VAN ROMP	LENGTE v. KOP	BREEDTE v. KOP		INDEKS BORS: SAG./TRANS.	INDEKS BUIK: OMV./L.L.			
21	22	23	24	25	26	27	28	29	30	$\frac{18 \times 100}{17}$	$\frac{24 \times 100}{1}$			

A STUDY OF MALE SOMATOTYPES AMONG THE SOUTH AFRICAN BANTU MINE LABOURERS COMPARED WITH OTHER GROUPS (SHELDON'S NOMENCLATURE)

by

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(With 8 Tables and 5 Text-figures)

Thesis accepted for the Master's Degree in Zoology
at the University of Stellenbosch

Submitted: March, 1959

ABSTRACT

The present investigation is a contribution to the incidence of the types of physical build of Tanganyika and Nyasa mine labourers at Johannesburg. Older norms of *Körperfüllenindex* were discarded in favour of that of Sheldon 1940, and the percentage distribution ascertained.

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INTRODUCTION

Much has been written about the variation in the human body-build. Just as there are no two persons of identical temperament or personality so are there never two identical bodies.

In the early history Hippocrates \pm 400 B.C., designated two fundamental physical types, which he called 'habitus phthisicus' and 'habitus apoplecticus'. Both names reflected a supposed relationship between physique and certain illnesses. This is the prototype for the modern conception of asthenic and pyknic types.

In the year 1509, Luca Pacioli, a Franciscan friar, published a book in which he propounded the 'divine' harmony of proportion, 'that the minor part is to the major part as the major part is to the whole'.

The great masterpiece of Albrecht Dürer was published in 1528. At the time of his death he was preparing a work called "The Four Books of Human Proportions". The illustrations reveal the relative proportions of geometrical segments.

As early as 1899, R. Livi, the Italian anthropologist developed the 'Index Ponderalis', which, in modified form, is the 'Körperfüllenindex' of Rohrer.

In about 1909, Viola took the lead in anthropometric studies and by his methods distinguished three morphological types, namely microsplanchnic, normosplanchnic, and macrosplanchnic. This agrees with the 'habitus phthisicus', an intermediate variation, and the 'habitus apoplecticus'. Many analogous classifications have been suggested, such as Sigand's (1914) 'respiratory', 'muscular' and 'digestive' types.

Kretschmer in 1921 revived the Greek terms of pyknic and asthenic for describing the macrosplanchnic and the microsplanchnic physiques respectively. He also suggested a third type which he called the athletic. According to him most individuals consist of a mixture of these three types in varying proportions.

Sheldon, 1940, elaborated Kretschmer's observations and found the variables to be related with the degree of development of the derivatives corresponding to each of the three embryonic layers. He named them endomorphy, mesomorphy and ectomorphy. He related each of his three types not only to human temperament, but also to classification of mental disorders, differential food needs and delinquency. Endomorphy means predominance of soft roundness throughout the various regions of the body. Mesomorphy means predominance of muscle, bone and connective tissue. Ectomorphy means predominance of linearity and fragility.

The three components of each variant are rated to a 7-point scale, on which the value 4 indicates the midpoint. An extremely endomorphic body-build, corresponding to Kretschmer's pyknic type would be 7-1-1, which denotes that the first component, endomorphy, is strongly developed while the mesomorphic and the ectomorphic components are extremely weakly developed.

The variants of body-build occur in both sexes with certain variants more common among males, and others among females. Sheldon (1940) stresses the point that males are as a rule higher in mesomorphy than females.

The classification of body-build is still one of the most controversial problems in constitutional research. In the problems of race, growth and constitution, the descriptive technique of anthropometry, anthroposcopy and photography, have all been used extensively by various research workers. After Sheldon's publication in 1940, other workers have reported on somatotypes in different segments of the population (Seltzer and Gallagher 1946, Bullen and Hardy 1946, Dupertuis 1950, Reynolds and Asakawa 1950, and Tappen 1950).

The individual of the modern age is required not only to absorb a good deal of technical knowledge, but he must also be able to apply it to his particular field. Although the physical functions in healthy people vary to a high degree, the general application of these functions is of great importance, particularly in the field of big industries, like mining.

The Bantu mine labourers come from all parts of Africa south of the Equator and their physical and mental qualifications are entirely different.

This paper presents an account and the results of an investigation of types of physique and their relative frequencies in a segment of the South African Bantu mine labourers. It is the first time that an attempt to investigate the morphological constitution of the Bantu, as reflected in the mine labourers population, has been made in South Africa.

ACKNOWLEDGEMENTS

This investigation was carried out at the Witwatersrand Native Labour Association, Johannesburg, in conjunction with other experiments done by the staff of the Applied Physiology Laboratory of the Transvaal and Orange Free State Chamber of Mines, together with the Anatomy Department of the Witwatersrand University. I desire to express my thanks to the W.N.L.A. for their co-operation and permission to carry out the study.

My sincere appreciation goes to the Director and staff of the Applied Physiology Laboratory for their interest and ready assistance, and I wish to express my gratitude to Dr. P. Tobias, head of the Anatomy Department of the Witwatersrand University, for his willing help.

Appreciation is also expressed to the Transvaal and Orange Free State Chamber of Mines for their permission to submit this paper.

I am indebted to Professor C. G. S. de Villiers, of the Zoology Department, Stellenbosch University, for his extremely valuable assistance, and helpful suggestions and criticisms during the preparation of this paper.

MATERIAL

This series represents two groups of material: 107 Tanganyikas and 139 Nyasas, totalling 246 subjects. The populations of these two areas are by no means homogeneous, tribally or linguistically, but culturally the tribes are very similar. The people of these tribal areas live primarily on the crops grown in their gardens (Mitchell, 1956). In the present study the numbers and percentages of tribes are as follows:—

TABLE 1

	Tribe	No.	%
Tanganyikas	Nyakyusa	56	52.3
	Kinga	3	2.8
	Ndali	11	10.2
	Inamwanga	5	4.6
	Others	32	29.9
Nyasas	Ngoni	15	10.9
	Yao	9	6.6
	Chewa	88	64.2
	Others	25	18.2

Only labourers who had never before been employed on the mines were chosen, and since age determination is not always accurate, the subjects were inspected for molar eruption. The selection was confined to subjects in whom all four molars were fully erupted. Occasionally, subjects with single molars not completely erupted were included in the groups.

The nature of the selection favours a high incidence of young males who have just completed the growth period and are rural in their eating habits and social economy.

The geographical distribution of some tribes is shown in Figures 1a and 1b.

METHOD AND TECHNIQUE

(i) *Photography*

The first important step was the standardisation of a photographic technique. A scale photograph of technical excellence offers a permanent record and a direct check on many observations. The photographic technique as an aid to description is not new. Martin (1914) gives detailed instructions for the taking of photographs, and workers contributing to various German journals (e.g. *Zeitschrift für Konstitutionslehre*, *Zeitschrift für Rassenkunde*) and to American journals (e.g. *American journal of Physical Anthropology*) make use of photographs.

The subjects stood on a pedestal so placed that the backs of their heels were 10 cms. from the centre of the platform. The feet were directed outwardly at about 45 degrees from the median plane. The pedestal is constructed to revolve between three stops placed at intervals of 90 degrees. In this way exact frontal, profile and dorsal pictures can be taken without any movement on the part of the subject. Three photofloods in reflectors were used and adjusted to the surroundings. The photographs were taken on Adox KB 21 film with a 35 mm. camera which was levelled on a tripod with the camera lens to subject, distance never less than 6 meters and never



FIGURE 1 A
DISTRIBUTION OF SOME TRIBES AFTER
COLSON & GLUCKMAN 1951

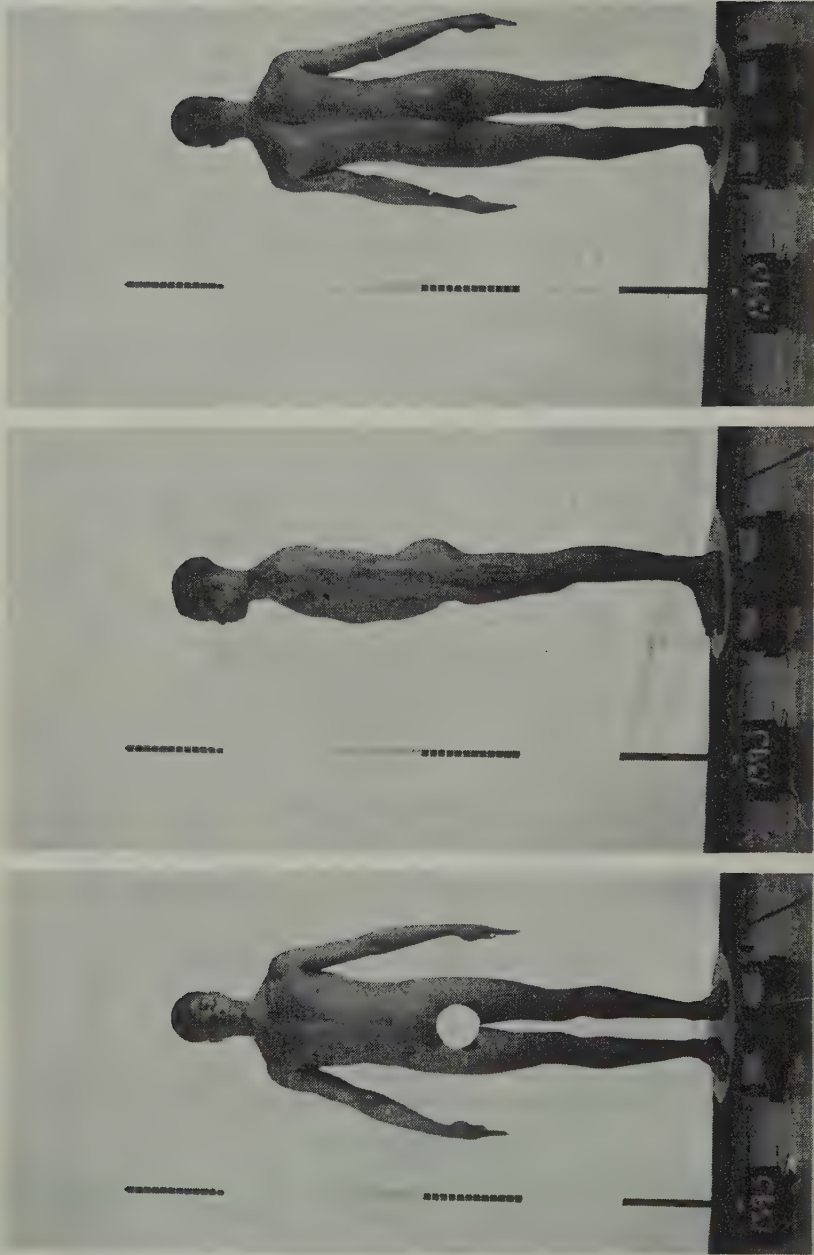
more than 7 meters. Cards with the subjects' numbers were placed on the floor against the foot piece of the surveyor's ruler which was used as a standard scale. With this equipment a series of standardised photographs of 246 males was taken. The technique used can be seen from the photograph on page 148.

Gavan et al. (1952) have shown that measurements can be taken from photographs and that these measurements are within the error of direct measurements, provided a distance of 20 ft. or more is maintained to avoid distortion.



FIGURE 1B

DISTRIBUTION OF SOME TRIBES AFTER
COLSON & GLUCKMAN 1951



The photographic technique as discribed in the text.

γ RATIO OF PHOTOGRAPHIC TO ACTUAL DIAMETER OF A
SPHERE 50 CMS. IN DIAMETER AT FOUR LENS TO
SUBJECT DISTANCES

Lens to Subject Distance ft.	Ratio
10	.996
20	1.000
30	1.000
40	1.000

γ Given by Gavan et al. (1952)

(ii) *Anthroposcopic Somatotyping*

Photographs served as a basis of a descriptive classification of the morphological components in the population studied. However, morphological description must be clearly presented before correlation can be attempted.

The list of inspectional criteria was prepared and used scopically to determine the relative strength of the three basic components in each of five regions of a given physique. The five regions are:—

Region I	— Head, face, neck
Region II	— Thoracic Trunk
Region III	— Shoulders, arms, hands
Region IV	— Abdominal trunk
Region V	— Legs and feet

A modified version of Sheldon's scopic method was used. This is based on a method evolved by Bullen and Hardy (1946) in their analysis of body-build photographs of American college women. Kraus (1952) used Bullen and Hardy's method in his study of Japanese. Danby (1953) applied modification and amplification because several of these criteria were vaguely specified or difficult to apply. In the present study a combination of the criteria of Bullen and Hardy and of Danby is used. It is felt that with this anthroposcopic method a closer comparison with other non-white groups will result. The criteria are listed in Table 2.

Irregularities in the posing led to certain occasional departures from the established procedure. In the lateral view, in order not to obscure the contour of the back, the left arm was sometimes flexed which could have been the result of:—

- (i) bad posing by author;
- (ii) marked lumbar lordosis on the part of the subject;
- (iii) overeating prior to being photographed;
- (iv) distension of abdomen caused by lordosis, as also found in at least 7% of Native East Africans (Danby, 1953).

Each subject was somatotyped scopically, region by region, on a thirteen point scale and the regional somatotypes were averaged in the following way:—

Example

Region I	—	4	3	$1\frac{1}{2}$
Region II	—	5	3	1
Region III	—	$4\frac{1}{2}$	4	2
Region IV	—	$4\frac{1}{2}$	3	$1\frac{1}{2}$
Region V	—	3	$4\frac{1}{2}$	3
		5	21	17.5
				9
Decimal Somatype		4.2	3.5	1.9
Final Somatype		4	4	2

DYSPLASIA

9	
8	
9	
—	
26	Total Dysplasia
—	

In the final somatype for the body as a whole, I dropped the decimal .3 and carried .4 as 1.0. Then the total dysplasia, which was defined as an inconsistent or uneven mixing of the three components in different regions of the body, could be calculated. This is called the 'd-index' and is the sum of the differences between each region of the body and these differences, for all three components must be added together.

There is now a way of referring numerically to the dysplastic aspect of an individual's physique. In a big series the third component shows more dysplasia than the second, and the second shows more than the first. With dysplasia the morphological conflict can perhaps be measured.

TABLE 2

List of inspectional criteria used in this study. (The same number under each Region for each of the three components deals so far as possible with an equivalent anatomical feature or area. The criteria are based on a combination of that used by BULLEN AND HARDY (1946) and by DANBY (1956).)

ENDOMORPHY

Region I — Head, Face and Neck

- 1 Little bony relief; muscling not marked.
- 2 Fat cheeks; face wide.
- 3 Soft round features — lack of extreme heaviness, muscularity or boniness.
- 4 Smooth short neck.
- 5 Clavicular outline softened; shoulder girdle padded.
- 6 Large antero-posterior approximates to transverse diameter of neck.

Region II — Thoracic Trunk

- 1 Back smooth; no muscle relief.
- 2 Back not narrowing to waist.
- 3 Fatty pectoral area.
- 4 Side view abdomen 'flabby'.
- 5 High position of lower ribs — tends to short chest cage.

Region III — Shoulders, Arms and Hands

- 1 Shoulders high and soft, sometimes sloping.
- 2 Proximal arm segments heavy and the thickness greater than distal.
- 3 Smooth upper arm and tapering lower arm.
- 4 No bony projections and wrists rounded.
- 5 Soft, pudgy hands.

Region IV — Abdominal Trunk

- 1 Full, fat abdomen — large antero-posterior diameter.
- 2 Waist high and wide.
- 3 Broad pelvis; fat on upper thigh projects laterally from buttocks.
- 4 Buttocks soft, round and large.
- 5 Fat folds in front and side views.

Region V — Legs and Feet

- 1 Proximal leg segments heavy with pneumatic fullness.
- 2 Little or no bony and muscle relief.
- 3 Predominance of outer calf curve.
- 4 Ankles fat.
- 5 Small plump feet.

MESOMORPHY

Region I — Head, Face and Neck

- 1 Muscular, rugged head and face, not linear or fat.
- 2 Massive cheek bones; square and strong face.
- 3 Heavy features.
- 4 Pyramiding of trapezius muscles on side of neck.
- 5 Clavicles heavy, prominent.
- 6 Antero-posterior diameter approaches transverse diameter of neck.

Region II — Thoracic Trunk

- 1 Rugged muscling, back and front.
- 2 Broad back; chest wide and tapers to base (shows usually in both back and front views).
- 3 Muscular pectoral area.
- 4 Thorax predominates over well muscle-controlled abdomen.
- 5 Heavy well-muscled ribs; moderate rib angle.

Region III — Shoulders, Arms and Hands

- 1 Shoulders rugged and broad; sometimes slope from trapezius.
- 2 Arm segments evenly proportioned with well developed deltoids, triceps and biceps.
- 3 Forearm thickness approximates upper arm thickness.
- 4 Joints prominent and wrists massive.
- 5 Well muscled hands, length of fingers variable.

Region IV — Abdominal Trunk

- 1 Compact well-muscled abdomen. Antero-posterior diameter less than transverse.
- 2 Low well-muscled waist, medium width.
- 3 Heavy, sturdy pelvis; firm muscled thigh.
- 4 Muscular buttocks, laterally dimpled.
- 5 Distinct line in the inguinal region.

Region V — Legs and Feet

- 1 Even muscular development of proximal and distal segments; thighs well-muscled.
- 2 Large knee joints and thick bony ankles.
- 3 Lateral muscling of thighs predominant.
- 4 Pronounced development of inner gastrocnemius.
- 5 Heavy bony feet.

ECTOMORPHY

Region I — Head, Face and Neck

- 1 Head slight and linear.
- 2 Thin, fragile-boned face.
- 3 Sharp, finely chiselled features.
- 4 Slender neck; sometimes inclined forwards.
- 5 Delicate, sharp clavicles.
- 6 Small antero-posterior diameter approaches transverse diameter of neck.

Region II — Thoracic Trunk

- 1 Back bone; slight thready muscles, back and front.
- 2 Narrow back; slight to medium taper.
- 3 Flat, bony pectoral area.
- 4 Thorax narrower and longer than abdomen; scapulae winged out.
- 5 Skinny ribs, sharp rib angle.

Region III — Shoulders, Arms and Hands

- 1 Shoulders narrow, bony and thin — sometimes high.
- 2 Arms long, particularly distal segments.
- 3 Stringy muscles in upper arms and weak forearms.
- 4 Small joints with fragile, narrow wrists.
- 5 Slender hands and fingers.

Region IV — Abdominal Trunk

- 1 Small non-muscular abdomen; short compared with long arms and legs.
- 2 Waist region non-muscular; slim.
- 3 Light, narrow pelvis with relatively flat buttocks.
- 4 Flat abdomen may protrude below navel.
- 5 Stringy muscle relief; ant. sup. iliac spine visible.

Region V — Legs and Feet

- 1 Legs relatively long, particularly distal segments.
- 2 Weak muscling of thighs.
- 3 Legs spindly with space between thighs when heels together.
- 4 Little muscling of calves; narrower, delicately boned ankles.
- 5 Slender delicate feet.

RESULTS AND DISCUSSION

(i) Distribution of the Somatotypes

We now consider the number of physiques in a population of 246 cases that fall within a total of 44 somatotypes. The distribution is recorded in Table 3. Danby, in a sample of 219 Native East Africans, found 37 somatotypes, compared with the 76 in Sheldon's sample of 4,000 European American students, and 25 in Kraus's sample of 544 Japanese.

The majority of the present sample of Bantu (77.56%) was grouped within seventeen somatotypes, e.g. 442, 343, 253, 353, 263, 344, 244, 144, 254, 154, 164, 345, 245, 145, 255, 155, 246. Of these, the six most frequently encountered together represented 56.93% of the sample.

In the present series, eleven somatotypes do not occur in Sheldon's European sample. All together they represent 13.74%. Of the somatotypes which are absent in Sheldon's sample, Kraus found 4.7% among the Japanese group. The thirty-three somatotypes which are common to the present series and that of the Sheldon series, account for 85.9% of the former and 59.1% of the latter.

Although nineteen somatotypes of the present series do not occur in Danby's 219 East Africans, the twenty-five which are common to both series, account for 72.56% of the former and 75.69% of the latter. The most frequently occurring somatotypes in the present sample are 254 (12.19%) and 145 (12.19%), whereas in Danby's East Africans the highest incidence is 11.4% for somatotype 253.

Tanner (1954) has stressed that "... trained observers using the technique of anthroposcopic somatotyping agree in their ratings on healthy men aged 18—30 to within half a rating on a 7-point scale in 90% of instances. In 10% of instances observers differ by as much as one rating unit; very seldom indeed do they differ more than this." (p. 261).

TABLE 3

Somatotype	Tanganyika No.	Nyasa No.	Nyasa %	Total Sample No.	Total Sample %	Danby's 219 East Africans No.	Danby's 219 East Africans %	Sheldon's 4,000 Europeans No.	Sheldon's 4,000 Europeans %	Kraus's 544 Japanese %
521		1	0.71	1	0.40	—	(19not)	—	(11not)	—
541	2		1.86	2	0.80	—	—	13	0.3	—
551		1	0.71	1	0.40	—	—	5	0.1	0.4
451	1		0.93	1	0.40	—	—	13	0.3	7.5
261		1	0.71	1	0.40	1	0.45	27	0.7	3.9
171	1	1	0.93	2	0.80	—	—	20	0.5	0.2
442	4		3.73	4	1.62	3	1.40	117	2.9	0.9
342	2	1	1.86	3	1.21	16	7.30	—	—	3.7
452	1	1	0.93	2	0.80	—	—	92	2.3	1.3
352	1	2	0.93	3	1.21	11	5.00	92	2.3	8.3
252		3	2.15	3	1.21	14	6.40	33	0.8	10.3
462	1		0.93	1	0.40	—	—	—	—	0.5
262	1	1	0.93	2	0.80	11	5.00	91	2.3	2.4
162	1	1	0.93	2	0.80	—	—	24	0.6	—
172		1	0.71	1	0.40	—	—	21	0.5	—
343	2	3	1.86	5	2.03	5	2.30	189	4.7	0.7
253		15	10.79	15	6.09	25	11.40	133	3.3	—
453	2	1	1.86	3	1.21	—	—	40	1.0	—
353	3	4	2.80	7	2.84	—	—	197	4.9	0.4
153		2	1.43	2	0.80	2	0.90	—	—	—
263		4	2.87	4	1.62	1	0.45	25	0.6	—
163		3	2.15	3	1.21	—	—	17	0.4	—

Table 3 contd.

TABLE 3 (contd.)

Somatotype	Tanganyika		Nyasa		Total Sample		Danby's 219 East Africans		Sheldon's 4,000 Europeans		Kraus's 544 Japanese	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
334	3	2.80			3	1.21	2	0.90	201	5.0	—	—
234	1	0.93			1	0.40	23	10.50	—	—	0.5	—
344	3	2.80	1	0.71	4	1.62	1	0.45	230	5.8	—	—
244	15	14.01	10	7.19	25	10.16	14	6.40	167	4.2	—	—
144	2	1.86	2	1.43	4	1.62	4	1.80	—	—	—	—
354	1	0.93	1	0.71	2	0.80	—	—	52	1.3	—	—
254	11	10.28	19	13.67	30	12.19	3	1.40	63	1.6	—	—
154	3	2.80	12	8.63	15	6.09	—	—	21	0.5	—	—
164	4	3.73			4	1.62	—	—	—	—	—	—
335	2	1.86			2	0.80	1	0.45	118	3.0	—	—
235	2	1.86	1	0.71	3	1.21	11	5.00	181	4.5	—	—
135			2	1.43	2	0.80	6	2.74	—	—	—	—
345	4	3.73			4	1.62	—	—	33	0.8	—	—
245	10	9.34	14	10.06	24	9.76	1	0.45	56	1.4	—	—
145	10	9.34	20	14.38	30	12.19	1	0.45	22	0.6	—	—
255	4	3.73	1	0.71	5	2.03	—	—	—	—	—	—
155	3	2.80	4	2.87	7	2.84	—	—	—	—	—	—
126	2	1.86			2	0.80	5	2.30	29	0.7	—	—
236	1	0.93	1	0.71	2	0.80	1	0.45	20	0.5	—	—
136			3	2.15	3	1.21	2	0.90	7	0.2	—	—
246	3	2.80	1	0.71	4	1.62	—	—	—	—	—	—
127	1	0.93	1	0.71	2	0.80	2	0.90	20	0.5	—	—
Total:	107	99.80	139	99.72	246	99.64	166	75.69	2,369	59.1	—	41.0

In discussing the 76 somatotypes, Sheldon expressed the warning that "... perhaps no living physique is a perfect example of a somatotype. The somatotype derives from an average of tendencies." (p. 141).

The somatotype and component rating incidence of the Bantu represented in the present series is clearly different from that of Europeans and also Japanese (Fig. 3).

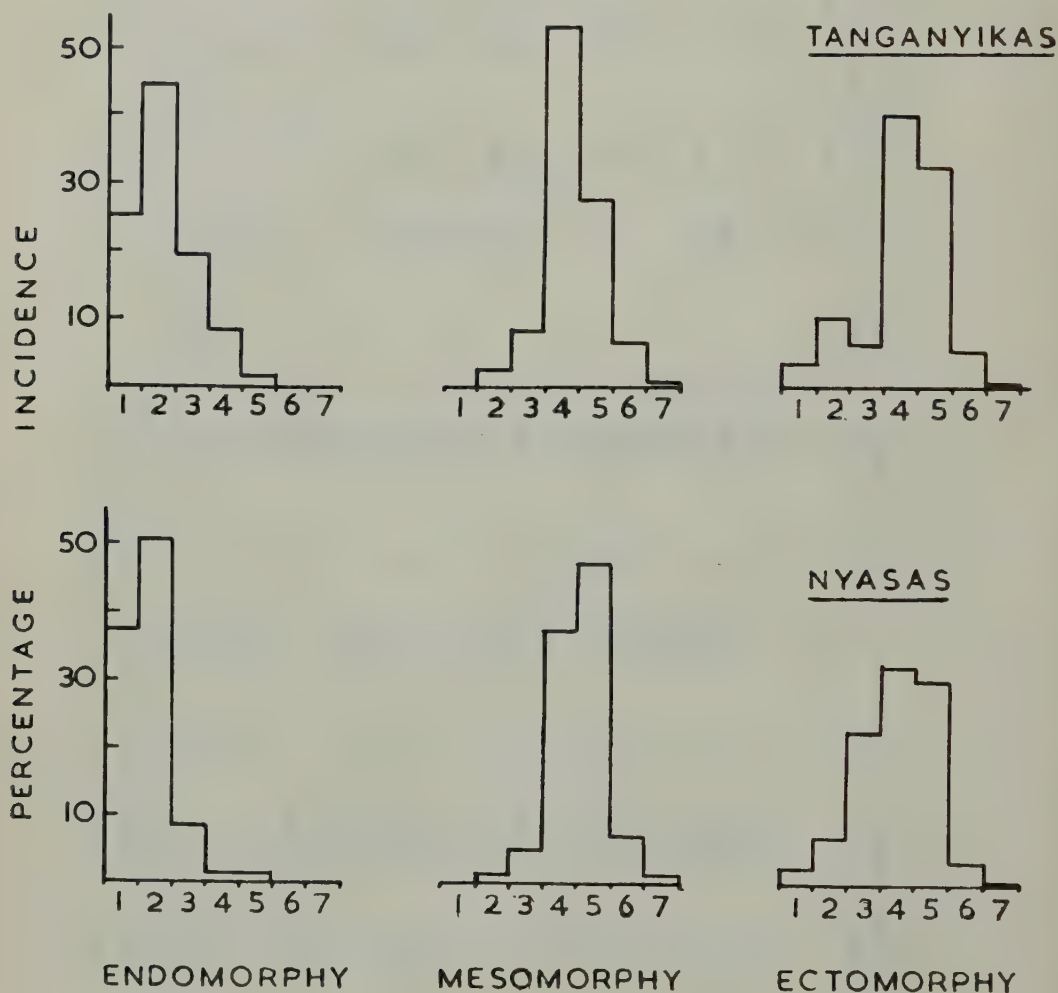


FIGURE 2 DISTRIBUTION FOR TANGANYIKAS 107
AND NYASAS 139

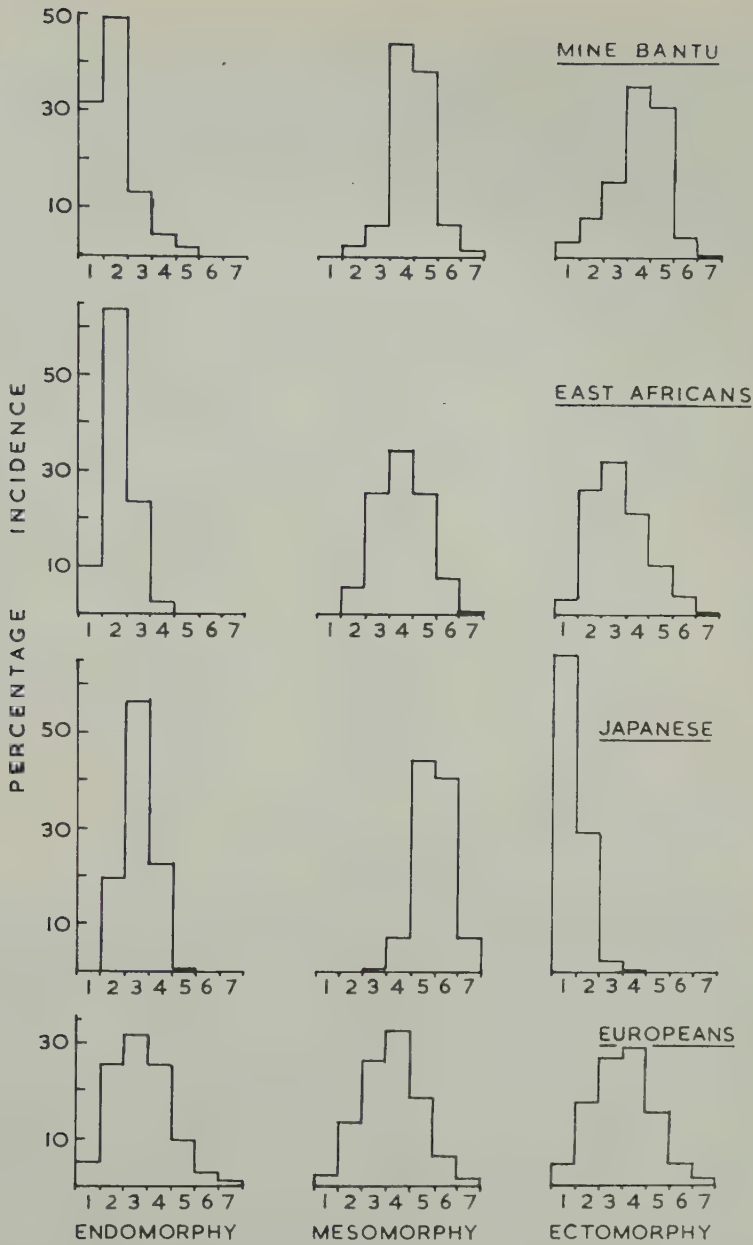


FIGURE 3 DISTRIBUTION FOR MINE BANTU, EAST AFRICANS-DANBY, JAPANESE-KRAUS, AND EUROPEANS-SHELDON

(ii) *Incidence of Components*

The frequency distribution of the various component ratings as estimated by the author and compared with results of some other workers, is given in Tables 4, 5 and 6. In the endomorphic component, the present series shows ratings which are very low. Ratings 1 and 2 have 81.27% incidence compared to 87.6% for ratings 2 and 3 of the Native East Africans. All the ratings are represented with the exception of ratings 6 and 7 which contain no subjects in this sample. The mean rating for the total series is 1.96 and the standard deviation 1.28.

TABLE 4

PER CENT. INCIDENCE OF ENDOMORPHIC COMPONENT				
Rating	Present Sample	219 East Africans (Danby) ³	544 Japanese (Kraus) ²	4,000 Men (Sheldon) ¹
1	31.98	9.95	0.2	5.0
2	49.29	63.95	19.8	25.1
3	13.34	23.65	56.5	31.9
4	4.43	2.30	22.8	25.1
5	1.60		0.7	9.5
6				2.6
7				0.8
	100.64	99.85	100.0	100.0
Mean	1.96	2.78	3.0	3.2
S.D.	1.28	.98	.67	1.2

1. Sheldon, p. 127

2. Kraus, p. 354

3. Computed by the author from Danby, p. 196

TABLE 5

PER CENT. INCIDENCE OF MESOMORPHIC COMPONENT				
Rating	Present Sample	219 East Africans (Danby)	544 Japanese (Kraus)	4,000 Men (Sheldon)
1				2.0
2	2.00	5.95		13.1
3	6.43	25.49	0.5	26.3
4	44.25	34.30	7.2	32.4
5	38.91	25.55	44.2	18.5
6	6.85	7.70	40.9	6.3
7	1.20	0.90	7.2	1.4
	99.64	99.89	100.0	100.0
Mean	4.4	4.0	5.4	3.7
S.D.	1.25	1.35	.75	1.2

The Bantu of the present sample have a higher mesomorphic rating than endomorphic rating. For the whole sample rating 4 represents the highest incidence of 44.25%, with rating 5 a close second with 38.91%. In the separate groups of Tanganyikas and Nyasas, rating 4 dominates in the former with 53.19% incidence and rating 5 in the latter with 47.39% incidence. Mesomorphy 3 and 6 follow with almost equal frequency in the whole sample and also the two separate groups. No individual has a rating of 1.

The mean mesomorphic rating for the entire series is 4.4 and standard deviation 1.25.

In the ectomorphic component rating the entire sample shows incidence of 35.71% and 31.25% at ratings of 4 and 5 respectively. The next most frequent ectomorphic rating is 3 with 15.80%.

TABLE 6

PER CENT. INCIDENCE OF ECTOMORPHIC COMPONENT				
Rating	Present Sample	219 East Africans (Danby)	544 Japanese (Kraus)	4,000 Men (Sheldon)
1	3.20	3.15	66.9	4.3
2	8.45	26.45	29.7	17.7
3	15.80	32.45	2.9	27.1
4	35.71	21.90	0.5	29.1
5	31.25	10.94		16.1
6	4.43	4.10		4.6
7	0.80	0.90		1.1
	99.64	99.89	100.0	100.0
Mean	3.9	3.2	1.3	3.5
S.D.	1.69	1.70	.57	1.3

For the two separate groups the incidence shows the same trend. The mean ectomorphic rating for the entire series is 3.9 and standard deviation 1.69. This shows a greater variability in ectomorphy than in the other two components.

The present sample is low in endomorphy and shows a high mesomorphic and ectomorphic dominance, with the mesomorphic component rating only slightly higher than that for ectomorphy.

Dominance in any component is not necessarily an indication of consistently high ratings for that component. Danby (1953) has shown in the Native East Africans that the rating for endomorphy rarely exceeds three. In the present series the endomorphic rating exceeds three in eight somatotypes only, with the result that dominance in both mesomorphy and ectomorphy must be enhanced. Danby records endomorphic ratings greater than three in only three somatotypes compared to Sheldon's thirty-seven and Kraus's nine. It is clear that endomorphy among all Bantu is consistently low.

In the Bantu the dominance of mesomorphy is emphasised by the low endomorphy.

The distribution of ectomorphy for the whole sample appears to be similar to that in Europeans. In the two separate groups it is especially the Nyasas who show great similarity in ectomorphy to that of Europeans, although the suggestion of lower ectomorphic ratings is stronger in the Bantu.

Sheldon writes: ". . . among the Negroes (400) it is the extreme second component that is most prominent and among the Jews it is the first, but a dominant third component is also prevalent in both groups." (p. 220).

The absence of high endomorphic ratings which can be seen in the histograms for this component too, suggests that certain factors are operating. These factors may be nutritional, environmental and genetic influence. Hot climates are generally associated with lower body weights in indigenous populations. (Roberts 1953).

The high mesomorphic rating of Kraus's Japanese and the absence of ectomorphy are possibly of genetic importance. The low endomorphy in the entire present series suggests a nutritional background, and agrees with the work of Keys et al (1950).

There are a number of limitations which must be kept in mind when comparing the values shown in tables 4, 5 and 6. The component ratings, as far as the technique is concerned, are arrived at by different methods, therefore the mean and standard deviations are probably not comparable. Another important point to be considered is the age difference between the groups. Sheldon's 4,000 European American male students range between 18—19 years, whereas Kraus's series of 544 Japanese must average close to 30 years (19—45 years). Here the difficulty arises that many Bantu do not know their own ages accurately. Danby claims that the major part (?) of the Native East African sample lies within the limits of eighteen to twenty-five years.

(iii) *Ponderal Index*

The range of the ponderal index (height over cube root of weight) reflects the absence of high endomorphs. In agreement with the work of Danby (1953), no values of the ponderal index below 12.0 were found among the Bantu of this series. In Danby's entire sample of Native East Africans there were only two subjects below 12.4, whereas in the two groups of the present series, nine Tanganyikas and ten Nyasas were found to be below 12.4.

The ponderal index is not infallible in attempts to classify body-build, for weight is subject to relatively great fluctuations in the heavier individual and depends upon the state of nutrition of the subject concerned. Table 7 gives for each somatotype the mean and the range of the ratio-index for height over cube root of weight.

Sheldon remarks:

"For somatotyping at later age levels, we shall probably attach less weight to this criterion (height over cube root of weight) . . ." (p. 266).

As it cannot discriminate between the weight of fat and muscle, in the present study the index correlates or not and is left at that.

(iv) *Dysplasia*

In the present study the dysplasia figures are computed by comparison of regional somatotypes as described by Sheldon. The dysplasia takes into

TABLE 7

Somatotype	Mean Height 107 Tanganyikas		Mean Weight 107 Tanganyikas		Mean $H/3/\sqrt{W}$ Tanganyikas	Range of $H/3/\sqrt{W}$ Tanganyikas
	Ins.	Cms.	Lbs.	Kgs.	English	English
521	62.8	159.6	135.5	61.3	12.2	12.2
541	—	—	—	—	—	—
551	64.4	163.6	135.0	61.1	12.5	12.5
451	—	—	—	—	—	—
261	66.0	167.8	156.0	70.6	12.2	12.2
171	—	—	—	—	—	—
442	60.5	153.8	112.5	50.9	12.5	12.0 — 12.9
342	62.9	160.0	117.5	53.2	12.8	12.7 — 12.9
452	65.9	167.6	132.0	59.7	12.9	12.9
352	64.0	162.8	146.0	66.1	12.1	12.1
252	—	—	—	—	—	—
462	66.4	168.9	134.0	60.7	12.8	12.8
262	64.9	165.1	148.0	67.0	12.2	12.2
162	61.1	155.4	125.0	56.6	12.2	12.2
172	—	—	—	—	—	—
343	63.0	160.2	130.0	58.8	12.3	12.3 — 12.4
453	64.5	164.0	122.0	55.2	13.0	12.9 — 13.1
353	64.3	163.4	123.0	55.7	12.9	12.5 — 13.1
253	—	—	—	—	—	—
153	—	—	—	—	—	—
263	—	—	—	—	—	—
163	—	—	—	—	—	—

TABLE 7 (contd.)

Somatotype	Mean Height		Mean Weight		Mean $H/3/\sqrt{W}$		Range of $H/3/\sqrt{W}$	
	107	107	107	107	Tanganyikas	Tanganyikas	Tanganyikas	English
	Ins.	Cms.	Lbs.	Kgs.				
334	63.1	160.4	118.3	53.5	12.9	12.9 — 13.2	12.9 — 13.2	12.9 — 13.2
234	67.5	171.7	130.0	58.8	13.3	13.3	13.3	13.3
344	62.8	157.9	121.6	55.0	12.7	12.7 — 12.8	12.6 — 12.8	12.6 — 12.8
244	64.2	163.3	119.8	54.2	12.9	12.9	12.4 — 13.7	12.4 — 13.7
144	64.2	163.4	122.0	55.2	12.9	12.9	12.8 — 13.0	12.8 — 13.0
354	64.1	162.9	117.0	53.0	13.1	13.1	13.1	13.1
254	63.1	160.4	119.0	53.9	12.7	12.7	12.4 — 13.0	12.4 — 13.0
154	63.7	162.1	121.3	54.9	12.8	12.8	12.7 — 13.1	12.7 — 13.1
164	63.8	162.3	120.7	54.6	12.8	12.8	12.5 — 13.2	12.5 — 13.2
335	61.4	156.1	108.0	48.9	12.8	12.8	12.6 — 13.1	12.6 — 13.1
235	65.7	167.0	116.0	52.5	13.4	13.4	13.2 — 13.6	13.2 — 13.6
135	—	—	—	—	—	—	—	—
345	63.8	161.8	107.7	48.7	13.3	13.3	13.3 — 13.4	13.3 — 13.4
245	64.8	164.7	119.3	54.0	13.1	13.1	12.9 — 13.5	12.9 — 13.5
145	64.7	164.6	118.4	53.6	13.1	13.1	12.6 — 13.8	12.6 — 13.8
255	65.6	166.9	129.5	58.6	13.0	13.0	12.6 — 13.3	12.6 — 13.3
155	66.8	169.9	129.6	58.7	12.9	12.9	12.7 — 13.2	12.7 — 13.2
126	65.8	167.2	108.5	49.1	13.8	13.8	13.8	13.8
236	67.9	172.5	122.0	55.2	13.6	13.6	13.6	13.6
136	—	—	—	—	—	—	—	—
246	66.6	169.3	118.2	53.5	13.5	13.5	13.5 — 13.6	13.5 — 13.6
127	61.3	155.8	93.0	42.1	13.5	13.5	13.5	13.5
Mean	64.2	163.4	123.5	55.9	—	—	—	—

TABLE 7 (contd.)

Somatotype	Mean Height 139 Nyasas		Mean Weight 139 Nyasas		Mean $H/3/\sqrt{W}$ Nyasas	Range of $H/3/\sqrt{W}$ Nyasas
	Ins.	Cms.	Lbs.	Kgs.	English	English
521	63.8	162.3	134.0	60.7	12.3	12.3
541	—	—	—	—	—	—
551	62.8	159.6	132.8	60.1	12.3	12.3
451	—	—	—	—	—	—
261	63.3	161.0	119.8	54.2	12.8	12.8
171	62.1	157.9	128.0	57.9	12.3	12.3
442	—	—	—	—	—	—
342	60.9	154.7	109.0	49.3	12.7	12.7
452	65.1	165.6	144.0	65.2	12.4	12.4
352	63.4	161.1	122.0	55.2	12.7	12.5 — 13.0
252	65.8	167.4	139.0	62.9	12.6	12.1 — 13.0
462	—	—	—	—	—	—
262	69.2	176.0	155.0	70.2	12.8	12.8
162	63.3	161.0	128.0	57.9	12.5	12.5
172	66.2	168.3	136.8	61.9	12.8	12.8
343	62.6	159.2	119.2	53.9	12.6	12.5 — 12.8
453	64.0	162.6	143.8	65.1	12.2	12.2
353	66.8	169.9	143.6	65.0	12.7	12.5 — 12.9
253	64.2	163.4	130.5	59.1	12.6	12.3 — 13.1
153	62.7	159.4	120.0	54.3	12.6	12.6 — 12.7
263	66.0	167.8	144.5	65.4	12.5	12.3 — 12.8
163	65.5	166.6	138.0	62.5	12.6	12.1 — 13.0

TABLE 7 (contd.)

Somatotype	Mean Height 139 Nyasas		Mean Weight 139 Nyasas		Mean $H/3 \sqrt{W}$ Nyasas	Range of $H/3 \sqrt{W}$ Nyasas
	Ins.	Cms.	Lbs.	Kgs.	English	English
334	—	—	—	—	—	—
234	—	—	—	—	—	—
344	65.6	166.7	124.8	56.5	13.1	13.1
244	65.3	166.1	127.2	57.6	12.9	12.3 — 13.3
144	65.3	165.9	121.5	55.0	13.2	13.2 — 13.3
354	60.7	154.4	108.0	48.9	12.7	12.7
254	65.9	167.8	130.6	59.1	12.9	12.3 — 13.4
154	65.0	165.3	128.2	58.0	12.8	12.5 — 13.2
164	—	—	—	—	—	—
335	—	—	—	—	—	—
235	63.8	162.3	114.0	51.6	13.1	13.1
135	68.0	172.8	124.9	56.5	13.5	13.2 — 13.9
345	—	—	—	—	—	—
245	65.1	165.6	119.1	53.9	13.2	12.8 — 13.7
145	65.0	165.2	116.2	52.6	13.2	12.7 — 13.8
255	66.5	169.1	129.0	58.4	13.1	13.1
155	63.3	161.0	117.5	53.2	12.8	12.6 — 13.2
126	—	—	—	—	—	—
236	68.3	173.7	128.0	57.9	13.5	13.5
136	64.5	164.0	111.2	50.3	13.3	13.1 — 13.5
246	67.8	172.3	137.0	62.0	13.1	13.1
127	69.8	177.5	132.0	59.7	13.7	13.7
Mean	64.9	165.1	128.1	58.0	—	—

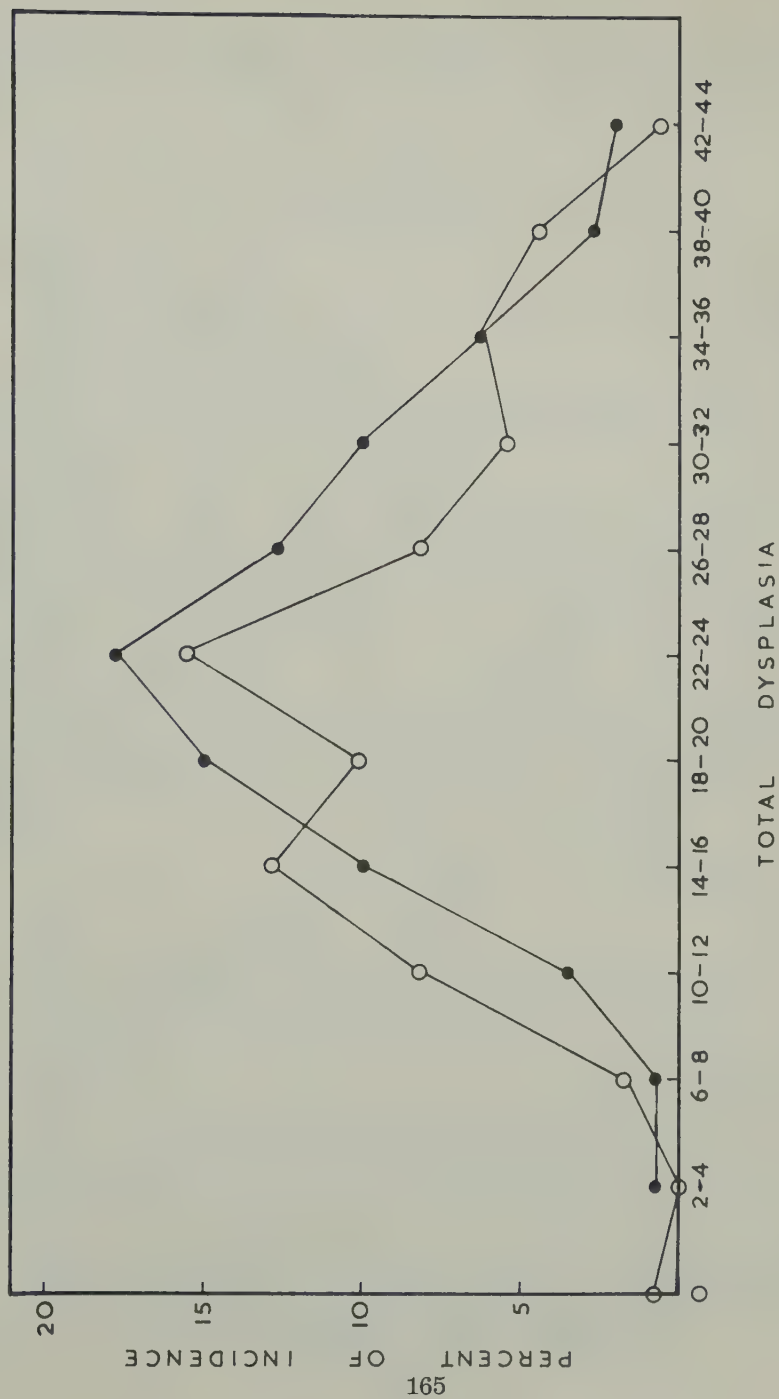
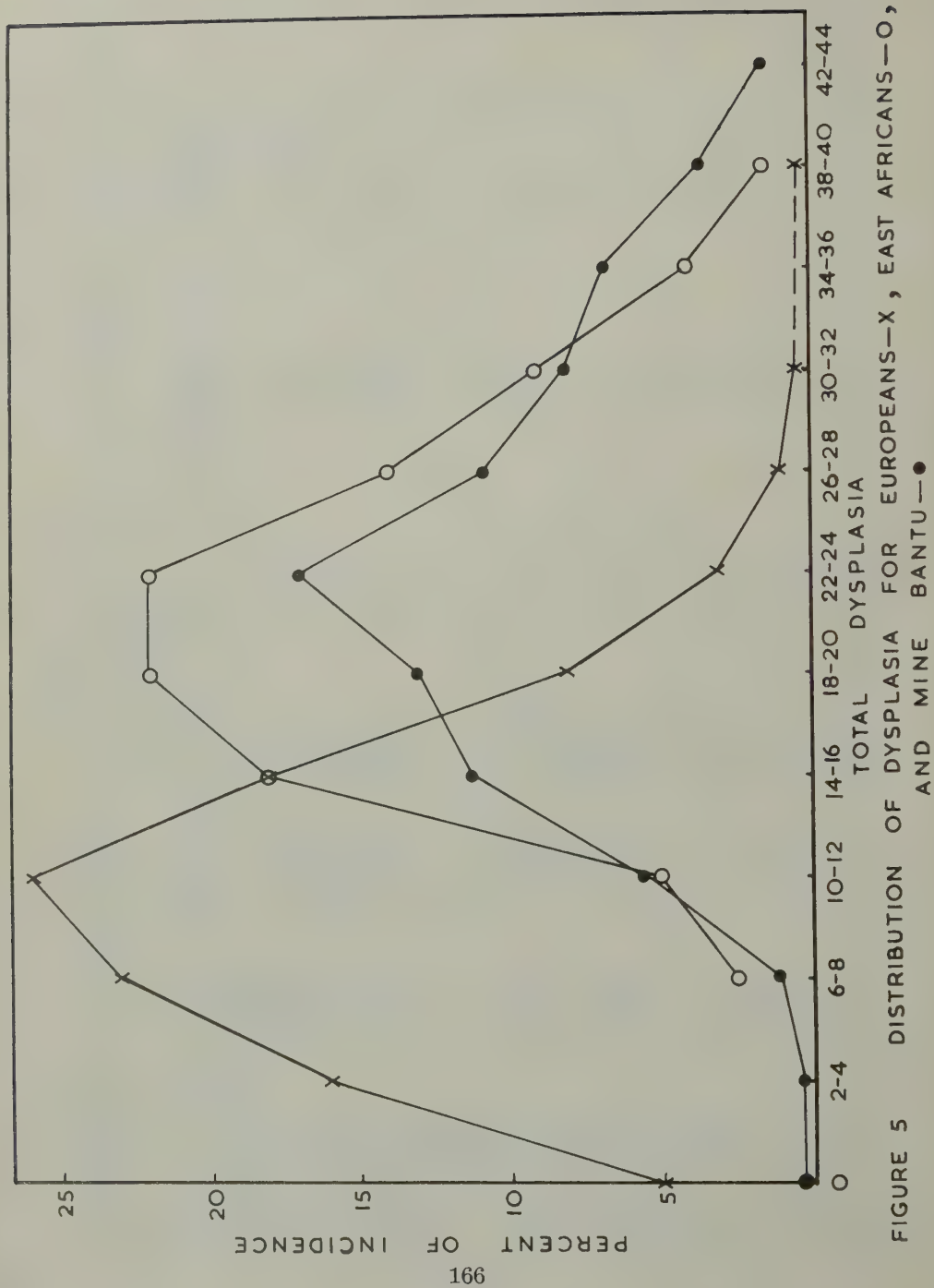


FIGURE 4 DISTRIBUTION OF DYSPLASIA FOR TANGANYIKAS—O AND NYASAS—●



account the differences for each component separately between each region of the body, but the difference in proportions of different parts of the body is not given by the total dysplasia. In Table 8 the mean total dysplasias are given.

TABLE 8
MEAN TOTAL DYSPLASIAS

Nyasas (107)	24.11
Tanganyikas (139)	22.82
Total Group (246)	23.57
Danby's East Africans (100)	21.77
Sheldon's Europeans (4,000)	10.29

The total dysplasia for the present sample is much higher compared with the 4,000 Europeans of Sheldon, but on the other hand agrees well with the figures given by Danby for Native East Africans.

In Figure 4, the incidence of total dysplasia can be seen for the two smaller groups. As the scopic scoring technique is not satisfactory for the estimation of regional dysplasia, some unevenness was found among the Tanganyika group which could result in the small difference between mean total dysplasias for the two groups.

Keys, et al. (1950) stressed the point of greater observer error in scopic regional assessments.

While Sheldon finds a range of total dysplasia for the 4,000 men from 0 to 36—40 and Danby finds the range for the Native East Africans from 6—8 to 38—40, the present total series reveals a range from 0 tot 42—44. The difference could be the result of the use of the anthroposcopic somatotyping method, which might affect the estimate of dysplasia (Tanner, 1952).

SUMMARY

The scopic somatotyping technique was applied to a sample of 246 mine Bantu, represented by two groups, e.g. 107 Tanganyikas and 139 Nyasas. The somatotypic analysis revealed the following:

According to the individual components, the present total series of Bantu was low in endomorphy with dominant mesomorphy, and medium to high in ectomorphy.

The Bantu physique was quite different from the European and the Japanese, as had been reflected by the sample studied.

A total of 44 somatotypes were represented of which the six most frequently encountered together represented 56.93% of the total sample.

The mean somatotype was 254 which represented 12.19% of the total sample.

The findings in incidence of somatotypes and of incidence of component rating were compared with Danby's 219 Native East Africans, Kraus's 544 Japanese and Sheldon's 4,000 European college males.

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* Not seen in the original

ON THE CLOACAL REGION OF ANURA in Particular of Larval *Ascaphus*

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(With 44 text-figures)

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Submitted: January, 1959

ABSTRACT

The ontogeny of the cloacal region of *Ascaphus* is described from limited larval material (beginning approximately at the stage of hind-limb bud development). A comprehensive series of *Bufo angusticeps* larvae and late pre-larval embryos were used for comparison. The adult and/or late larval conditions of the cloacal region in *Ascaphus*, *Bufo*, *Bombina*, *Leiopelma*, *Rana* and *Xenopus* are compared.

The rods of Noble supporting the cloaca in *Ascaphus* and the tendinous sheet connecting these with the epipubis are shown to be modifications of an interfemoral ligament present, with thickened lateral margins, in all the *Anura* studied. The cloacal lips differentiate early in metamorphosis in *Ascaphus* and *Bufo* and bear similar relations to the interfemoral ligament in these and other *Anura*, so that they are apparently homologous. The posterior part of the urodaeum is lengthened in the adult male *Ascaphus* to form the "tail" (phallus).

The hind-limb anlagen of *Ascaphus* appear directly beneath the spinal myomeres and immediately behind the posterior tips of the abdominal muscle cords. In *Ascaphus*, *Bufo* and *Bombina* the abdominal muscles (metamerically disposed in *Ascaphus* and *Bufo*) are initially attached posteriorly to the spinal myomeres but are separated from them anteriorly. It is probable that the mm. compressores cloacae are derived from the hind-limb anlagen. In all *Anura* examined, including members of all the South African families, the a. ischiadica and n. ischiadicus have a small muscle (designated m. circumflexor arteriae) associated with them; it is presumably capable of compressing the artery against the nerve.

The cloacal region of *Ascaphus* appears to be less specialized than that of *Rana* and *Xenopus*, contrary to what is generally believed for the last two genera. *Bufo*, particularly, and *Bombina* have undergone less specialization.

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INTRODUCTION

This investigation was undertaken at the suggestion of my promotor, Prof. C. G. S. de Villiers, and to his encouragement, particularly in the initial stages of the work, and his inspiration, its completion is largely due.

During the course of an investigation of the anatomy of the cloacal region of the adult male *Ascaphus*, including some details of the adult female and larvae, it was decided to attempt to determine the ontogeny of the cloacal structures from the limited *Ascaphus* larval material available. The present paper represents the results of this attempt.

As suggested by the title of the paper (van Dijk, 1955) in which the work on the adult male was recorded — "The 'Tail' of *Ascaphus*: A Historical Résumé and new Histological-Anatomical Details" — an attempt was made to review the literature on the cloacal region of *Ascaphus*.

As the paper was completed (and accepted for the M.Sc. degree) in March 1953, Bhaduri's work on the urinogenital system of the *Anura* (Bhaduri, 1953) which included an investigation of *Ascaphus*, and Ritland's studies (1955a and 1955b) on the post-cranial skeleton, nervous and muscular systems of *Ascaphus* were thus not discussed.

ENUNCIATION OF THE PROBLEMS

According to classic investigations the muscular layers of the mesenteron of *Chordata* are derived from the splanchnic mesoderm, which constitutes the mesial wall of the splanchnotome of each side, and the trunk and abdominal musculature develops in the somatic mesoderm, which constitutes the lateral wall of the splanchnotome of each side. By an investigation of the development of the (visceral) muscle layers of the coprodaeum at the coprodaeal-proctodaeal junction, and of the (somatic) abdominal muscle layers in the region of the proctodaeal aperture, the origin of the muscle-lining of the proctodaeum might be determined. The development of the tail musculature and of the muscles of the hind-limb might be relevant to this problem in view of their proximity to the proctodaeum. The relation of the coelom, posterior lymph sacs, pelvic girdle and urostyle, and of the blood vessels and nerves of the cloacal region, to the cloaca during development might provide important information on the development of the proctodaeum.

In *Ascaphus* the development of the cavernous tissue of the cloaca, of the (post-pubic) rods of Noble supporting the cloaca, and the muscle layers apparently dorsally striated and ventrally unstriated and associated with these rods (cf. van Dijk, 1955), merit investigation. The developmental origin of the mm. caudalipuboischiotibiales and (mm. pyriformes) and of the epipubis and mm. epipubici, might be relevant in view of the association of the former with the tail and hind-limb in the region of cloaca, and in view of the epipubis forming the posterior attachment of the abdominal muscles antero-ventral to the cloacal aperture (though separated from the latter by the pelvic girdle).

The distribution, forms and functions of the anterior slips of the mm. compressores cloacae extending from these muscles around the ischiadic

nerves and arteries in *Rana*, *Ascaphus* and *Xenopus*, present problems which require investigation, particularly as *Leiopelma* has no such slip arising from the m. compressores cloacae (van Dijk, 1955).

With a knowledge of the development of the proctodaeum of the *Anura* the evolution of the cloaca and copulatory organs of the *Amniota* might be capable of solution.

ACKNOWLEDGEMENTS

At the completion of my studies for the degree of Doctor of Science I would like to express my indebtedness to all, zoologists and non-zoologists alike, from whom I have received inspiration, learnt techniques and gained knowledge.

The inspiration of working both under Dr. de Villiers, and also with the research students he has taught, has been very great. The staff of the Zoological Institute, Stellenbosch (Dr. C. G. S. de Villiers, Dr. C. A. du Toit, Dr. C. S. Grobbelaar and Dr. M. E. Malan) have all helped to make my years of work there of the happiest.

The facilities of the Zoology Department, University of Cape Town were used during 1956; those of the University of Natal, Pietermaritzburg during 1957 and 1958. The use of these facilities is much appreciated.

MATERIAL

The larval *Ascaphus* material examined was available at the Zoological Institute, Stellenbosch, largely in the form of serial sections or remnants imbedded in paraffin-wax, these all being derived from studies by de Vos during 1938 (on *Leiopelma*) and van Eeden (1951). The six larvae used by de Vos were Haemalum bulk-stained and sectioned transversely. Those sections which were counterstained by her had usually been so treated with Eosin, occasionally with Light-Green, Bismarck Brown or van Gieson's Picrofuchsin; those not done by her were counterstained with Eosin during this study. The thicknesses of the sections in each series were not recorded by de Vos and were not always constant. The larvae of van Eeden, sixteen in number, were bulk-stained with Borax-Carmine and the sections (transverse except 1 sagittal series) were counterstained with Azan. The thickness of the sections cut by van Eeden, and those cut in the present study, were recorded and were usually uniform for each series. In addition to the material sectioned or imbedded by de Vos and van Eeden four *Ascaphus* embryos from Mason County, Washington (A. M. N. H. Nos. 50583 and 50586, 1930) were treated in the same manner as van Eeden's specimens, giving 3 frontal and 1 transverse series cut at 10 μ .

Thus of *Ascaphus* 4 embryos, 22 larvae, and (from the studies of de Villiers, 1933, and van Dijk, 1955) 3 adult males and 2 adult females were available as serial sections.

For comparative purposes 17 *Cacosternum capense* larvae, 9 *Bombina pachypus* larvae, 1 *Plethodon* sp. adult, 1 *Siphonops annulatus* adult, 1 *Ambystoma maculatum* (= *Amblystoma*) adult, 1 *Salmo fario* juvenile, 5 *Periophthalmus*

koelreuteri small adults, 1 *Homo sapiens* embryo (late indifferent/female? stage), and 200 specimens of *Bufo angusticeps* (representing all the recognizable stages) were sectioned. There were also available 1 series of a *Leiopelma hochstetteri* adult male (from Wagner, 1934a and 1934b), 1 series each of *Rana grayi* adult male and female, 2 of *Xenopus laevis* larvae and 1 juvenile *Xenopus laevis*, 1 of a *Bufo gariepensis* juvenile, 3 of *Breviceps* juveniles and a postmetamorphic *Arthroleptela* series.

Material utilized for dissection included numerous *Xenopus laevis* adults, and one adult of each of *Rana angolensis*, *Pyxicephalus natalensis*, *Phrynobatrachus* sp., *Heleophryne* sp., *Phrynomerus* sp., *Bufo regularis* and *Chiromantis xerampelina*.

TECHNIQUES

The techniques used frequently differed from those in general practice. They are therefore described at some length.

Ascapus, Leiopelma, Xenopus and Rana sections

The average thickness of the sections in each of de Vos's series was determined by means of the micrometer fine-focus of a microscope (checked against other microscopes). It was also done by assuming dermal glands to be spherical, measuring their diameters (by means of an eye-piece micrometer) and comparing these diameters with the number of sections which the glands occupied or in which they appeared, the terminal sections in which the glands appeared usually being assumed to be half-occupied. The second of these methods was found to be reliable, giving consistent results.

Drawings on thin paper at enlargements of 50 diameters, were made (usually of every 4th section) by means of a vertical slide projector, Zeiss Luminar lenses being used as they gave wide, flat and bright images. The drawings were rendered transparent with xylene, each was adjusted in position to correspond with those before (and sometimes after) it, and base-lines for reconstruction were then marked by drilling orientation holes through the piles of papers. Graphic reconstructions were then made (see Pusey, 1939) of left lateral aspects (denoted *norma lateralis sinistra*), and sometimes dorsal aspects (denoted *norma dorsalis*). Use was also made of liver base-lines in doing lateral reconstructions from van Eeden's series and from those cut from his wax blocks (which contained liver slices). These base-lines were found to be of little use for adjusting the orientation of successive sections, but useful in establishing a general trend in direction over long intervals. Liver base-lines were most useful in orientating where a skeletal structure appeared or disappeared in a series of sections, thereby affecting the extent to which each section stretched during mounting. Sections through the pelvic girdle often stretched less than those in front of, or behind, them, and the cloaca tended to stretch away from the tail in those sections in which it was not held by skin to it. (For liver base-line technique see van Eeden, 1951, and Schepers, 1938.)

For truer dorsal reconstructions the degree of skewness (sagittalness) of the transverse sections was estimated by measuring the distance between

distinct bilateral structures (such as the ilia) and the distance by which one of these preceded the other in the series of sections (number of sections occupied \times section thickness). The distances so measured gave the tangent (or cotangent) of the angle of skewness, so that the true mid-line of the reconstruction could be drawn and the mid-line of each drawing could be aligned to this. For some distorted sections two mid-lines were drawn through each drawing and the structures on which each mid-line was based (ventral and dorsal respectively) were then reconstructed separately.

Photomicrographs were made of significant sections in all the series reconstructed, the levels of the sections being indicated on the reconstructions. Photomicrographs were also made of instructive sections from series not reconstructed, these illustrating, for instance, statements not figured in the 1955 work, the scope of which was reduced for publication. Use was also made of photomicrographs instead of drawings for reconstructions, and proved to be time-saving and otherwise vastly superior where orientation difficulties were not prohibitive. Such difficulties with photomicrographs arose from the need to use the cheaper, relatively opaque, photographic paper, instead of film plates or film-type papers which would have made possible simultaneous comparison of a greater number of photographs.

Where orientation difficulties were not great (e.g. where the notochord could be assumed to be straight, or in dorsal views) reconstructions were also done successfully by projecting the image of each section onto the reconstructing board, adjusting it to a base-line (e.g. notochord for lateral, and mid-line for dorsal, views), and to a vertical or horizontal line; then proceeding as usual with the image substituted for the usual drawing or photomicrograph.

Certain of the sections of Prof. de Villiers's specimens of adult *Ascaphus* male and female, which had been stained with Haemalum and van Gieson's Picrofuchsin, were restained with 1% aq. Light Green or van Gieson's Picrofuchsin followed by 1% aq. Light Green. The same treatment was given to sections through the cloacal region of the other adult female *Ascaphus*, which had been stained with Borax-Carmine-Azan, and to sections of the *Xenopus* adult after removal of the Eosin which had been used as counterstain to Haemalum. The Acid Fuchsin (of the van Gieson's Picrofuchsin) stained the collagenous connective tissue red, while the Light Green was taken up by non-collagenous connective tissue and by muscle. The greater affinity for Picric Acid (of the van Gieson's Picrofuchsin) of striated muscle, and, to a lesser extent, of unstriated muscle, resulted in a grass-green tinge (Light Green + Picric Acid) in the muscles as compared with a blue-green colour in the non-collagenous connective tissue. The Light Green was employed for $\frac{1}{2}$ to 1 minute and differentiated in water to give the correct overall colour on the section (approximately 15 secs. to 1 min.). Van Gieson — Light Green, Picro-Indigo-Carmine, Picro-Nigrosin and Retterer's Alum Carmine were employed on sections through the cloacal region of the male adult *Ascaphus* and on the female adult *Ascaphus* sectioned for that work.

The developmental stages of *Ascaphus* of which reconstructions were made have been numbered according to the criteria used for *Xenopus laevis* in the Hubrecht Laboratory publication "Normal Table of *Xenopus laevis* (Daudin)" (Nieuwkoop & Faber, 1956). For the stages up to stage 57 reference was made to the hind-limb development, for the later stages the

conditions of the opercula and fore-limbs were used. (The hind-limbs of the later stages of de Vos's material were incomplete distally.)

Bufo angusticeps material (and Bombina, Cacosternum, Ambystoma, Plethodon, Siphonops, Salmo, Periophthalmus and Homo)

The *Bombina*, *Salmo* and *Periophthalmus* specimens after fixation in Bouin's fluid, and the rest, except *Bufo*, after formalin fixation, were all treated much as described below for *Bufo*.

The *Bufo angusticeps* material was identified by reference to de Villiers (1929) and Noble (1926) initially; subsequently by the time of the year at which oviposition took place, the form of the egg-strings, and also by the dark pigmentation of the eggs and larvae (apparently darker than that of any other South African anuran). The material was killed and fixed in Lenhossek's Picric Acid — Mercuric Chloride — Acetic Acid — Alcohol solution, washed after 24 hours, decalcified (in some cases) in 5% Nitric Acid in 70% alcohol, stained in Grenacher's Borax-Carmine (except alternate early stages, which were Haemalum bulk-stained), dehydrated (sometimes only to 96% alcohol), cleared in Methyl Benzoate-Celloidin, impregnated for a half-hour in Benzol Wax at about 30°C, impregnated in vacuo in 52°C paraffin wax and imbedded and sectioned in fresh 52°C wax. The animals, whole or with only a part of the tail missing, were sectioned frontally most often, transversely least often, the relative numbers (excluding the earliest stages) being 74 frontally, 54 sagittally, 39 transversely, i.e. approximately 4 Frontal: 3 Sagittal: 2 Transverse series of *Bufo*.

Counterstaining of the *Bufo angusticeps* material was done with Heidenhain's Azan (except the Haemalum-stained early stages, for which Eosin was used). In addition 1% aq. Light Green was used for most of the older, and some of the younger, specimens. It was found that it facilitated recognition of striated muscle, non-collagenous connective tissue and nerve fibres. Striated muscle stains a characteristic orange-brown (similar to Bismarck Brown in hue) because of its affinity for both Orange G (from the Azan) and Light Green; non-collagenous connective tissue is stained blue-green, and nerve fibres a characteristic grey-green. The blue of collagenous connective tissue (Aniline Blue from the Azan) and the pink of unstriated muscle fibres (Borax-Carmine) are little affected by Light Green unless this is employed for too long. The use of Light Green derived from a suggestion of Prof. de Villiers that it be used as a counterstain to Haemalum. Safranin (= "Safranelin"?) was tried as a stain for non-collagenous fibres (Maskor, 1953), but seemed unsuitable for immature anuran tissue.

Limited use was made of base-lines, these being produced by boring holes at right angles to the plane of sectioning in wax blocks and filling the resulting holes in the sections with Indian ink. Wax models such as those described in the earlier paper (van Dijk, 1955), and photomicrographic stereograms similar to the graphic stereogram used in that paper (op. cit., fig. 29), were used to visualize the milieu of the cloaca and associated structures. The photomicrographic stereograms were produced by distorting photomicrographs by means of specially constructed anamorphote lens systems (which have since become familiar in connexion with "cinemascope").

Dissections of members of each of the families of South African Anura

After a number of different approaches to the cloacal region of *Xenopus* had been attempted, median incisions through the skin were made, extending half the way along the back above the cloacal aperture in all the specimens (*Xenopus* and others) dissected. This was followed by a median incision through the membrane over the urostyle. It was then usually possible to separate the fat containing the coccygeal lymph hearts and the septum iliacum mediale of one side, intact; this separation being achieved by carefully loosening these from the m. coccygeo-iliacus, and hooking them laterally whilst the urostyle and m. coccygeo-iliacus were hooked over to the opposite side. This dissection exposed the cloaca in dorsal and lateral view. Using a hooked needle, it was possible, in numerous *Xenopus*, to locate the dorsal aorta and pull it sideways so that the fluorescein injection technique used by de Graaff (1957) could be applied, the injection taking place after the dorsal aorta had been returned to its natural position with the needle in it. Thus blood-flow in the aa. iliacae could be watched under ultraviolet light.

PROCEDURE

As complete a series of *Ascaphus* as could be obtained from the available material, was made. Similarly, as complete a series of *Bufo angusticeps* was prepared as was possible from the specimens sampled at intervals during development. Extra specimens of *Bufo* at each sampling were preserved in wax ready for sectioning, should it be necessary. The comparative material listed above was then prepared.

Reconstructions of all the discernible features of as much of the pelvic region as possible, were made of all the *Ascaphus* stages that could be reconstructed. Of the *Bufo angusticeps* material, reconstructions of the salient features of the entire animal were made at the stages which marked the first appearance, and which illustrated the development of, the proctodaeum, the permanent gut lumen (unoccluded by yolk), the pronephric ducts, the abdominal muscles, the limb-buds, and the cloacal muscles.

Conclusions on the *Ascaphus* material were arrived at, illustrated and noted. These conclusions were checked on the *Bufo angusticeps* material and illustrated with further notes. Only then was the relevant literature thoroughly examined. This was done in an attempt at avoiding "anticipatory set", which produces subjectivity of approach, particularly in perception. Finally the material was re-examined together with the other animals prepared.

In presenting the results an attempt has been made to reproduce the evidence on which descriptive statements were based. Photomicrographs serve both to illustrate features and to check on the necessarily somewhat subjective reconstructions.

It must be noted that, while the *Ascaphus* material has been described at length and the *Bufo* material cursorily, the preparation and examination of *Bufo angusticeps* stages represented more than half of the work involved in this study. Without recourse to *Bufo angusticeps*, representing the typical anuran condition, the *Ascaphus* material could not have been adequately interpreted or described.

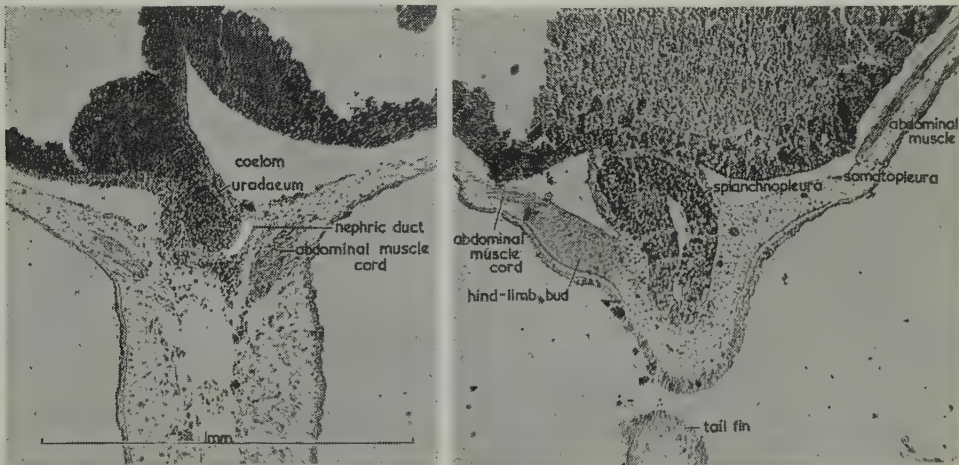
Note on Terminology

Gadow's (1887) terminology for the cloaca of *Amniota* has been adopted. The cloaca is thus considered to consist of a terminal ectodermal *proctodaeum*, a *urodaeum* into which the urinary and genital ducts and the bladder open, and a *coprodaeum* receiving the intestine. The use of this terminology implies that the urodaeum and coprodaeum are accepted as being of endodermal origin, for these parts of the cloaca are distinguishable in *Amniota* internal to the cloacal membrane (which represents the limit of the ectodermal proctodaeum) before this membrane perforates. That the urodaeum and coprodaeum are of endodermal origin in the *Anura*, appears to be established by evidence, presented below, that the urinogenital ducts open into an endodermal part of the cloaca.

DESCRIPTION OF THE STAGES IN *ASCAPHUS*

Stage 47 (figs. 1 and 2)

The nephric ducts open into the urodaeum at the posterodorsal margin of the coelom (fig. 1). Behind the urodaeum the proctodaeum is largely isolated from the inner, splanchnic, wall of the splanchnotome. The coelom extends furthest posteriorly along the gut laterally (fig. 2), ventrally not reaching as far posterior as the openings of the nephric ducts. From their ventral situation in the body-wall anteriorly the abdominal muscles pass dorsally caudad, separating the hind-limb buds partially from the coelom anteriorly (fig. 2, left), and completely from the myomeres of the tail antero-dorsally (fig. 1), attaching to these myomeres at the level of the nephric aperture.



Figs. 1 and 2.
Ascaphus embryo, Stage 47. Cloacal region (norma dorsalis).
Photomicrographs of frontal sections x 50.

Stage \pm 50 (figs. 3 and 4)

The relations of the segments of the abdominal muscles to the myomeres of the tail and trunk are well shown in the specimen at this stage. The posterior-most segment of the abdominal muscle is applied to the ventrolateral face of the myomere corresponding to the 9th spinal nerve (here referred to as the 9th *spinal myomere*). The second abdominal muscle segment from the posterior end is lateral to the coelom and ventrolateral to the 8th spinal myomere. The posterior-most abdominal segment is anteriorly mediad to that in front of it, but is lateral to it further posteriorly. The 9th and subsequent spinal myomeres curve ventrally round those behind them and extend dorsally on the inner faces of the latter. A few muscle fibres occur mediad to the posterior tip of the posterior-most abdominal myomere.

The coelom extends to near the posterior edge of the 9th spinal myomere posteriorly; medially it extends between the 9th spinal myomeres further dorsally than the level of the top of the last abdominal myomere. Laterally the coelom extends posteriorly almost to the posterolateral margin of the 8th spinal myomere dorsally, extending beyond this margin further ventrally.

Figs. 3 and 4.

Ascapus larva, Stage \pm 50 (both figs. from one specimen).
Posterior abdominal region x 25.

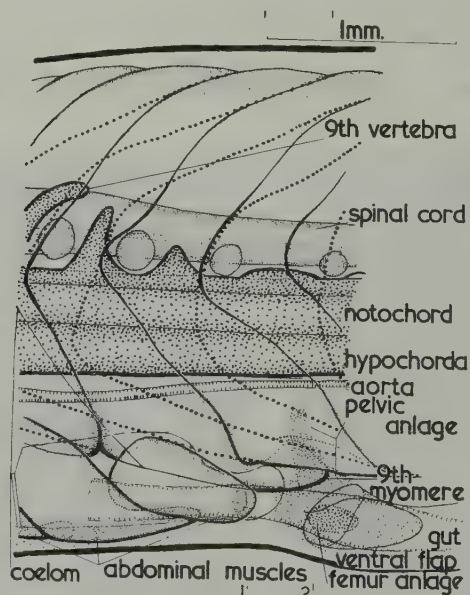


Fig. 3.

Norma lateralis sinistra.
Graphic reconstruction from
transverse sections.

The 8th spinal and abdominal myomeres are thus separated by coelom at this stage.

Hind-limb buds are visible at this stage and a femur anlage is present near the base of each. The concentrations of cells of each limb anlage extend anteroventrally to just anterior to the posterior limit of the coelom. Laterally each anlage extends anterodorsally over the posterior tip of the 9th spinal myomere onto the lateral face of the 10th spinal myomere. From this part of each limb anlage the ilium and associated structures will differentiate.

Mediodorsal and medioventral to the hind-limb buds are cell aggregations, the latter clearly constituting the anlagen of the rods of Noble.

The hypochord in the specimen is much thicker than in all other larvae examined, and the difference may not be developmental, but specific.

The myomeres and nerves of the specimen were numbered from the vertebral arches, the most anterior shown in fig. 3 being found, by counting, to be the 9th. At this stage the 9th arch is well-developed, but dorsally incomplete.

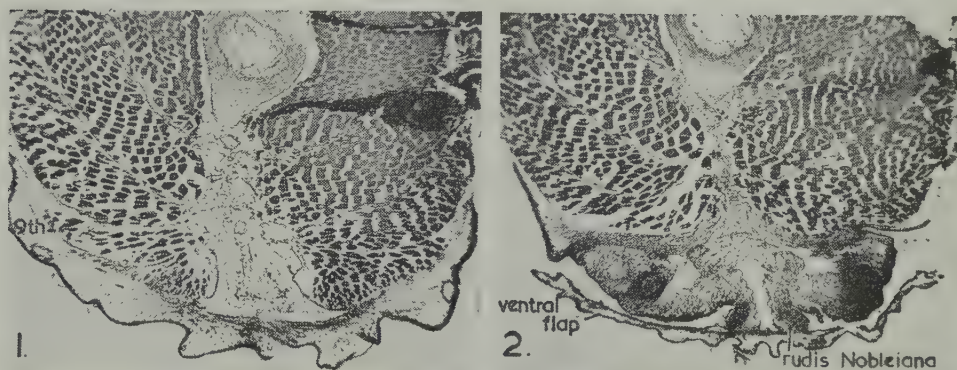


Fig. 4.

Norma posterioris. Photomicrographs of transverse sections.
(The numbers refer to levels in fig. 3.)

Stage 51 (figs. 5 and 6)

The proctodaeal aperture is situated on the dorsal surface of a flap of skin which covers the hind-limb buds ventrally and protrudes beyond them posteriorly. The aperture is roughly triangular, with the base near the posterior tip of the ventral flap, and the apex anterodorsal to this. Just anterior to the apex of the proctodaeal aperture a ventral projection from the tail attaches to the dorsal surface of the proctodaeum; anterior to this point the proctodaeum, and the flap of skin ventral to it, are suspended from the tail. Anteriorly the furthest limits of the proctodaeum are marked dorsally by the opening of the nephric ducts, ventrally by a thickening which represents the bladder. The coelomic cavity does not extend ventrally beyond the bladder, but dorsally the median urinogenital aperture is now a short distance

from the end of the coelom, which extends to the level of the 12th spinal nerve. The circular muscle layer present around the coprodaeum is continued in the urodaeal region; but it is interrupted dorsally where the nephric ducts join and enter the urodaeum, and ventrally at the bladder. Posterior to the nephric ducts the dorsal wall of the gut slopes down steeply, the circular muscle layer again becoming continuous dorsally where this slope decreases, which is still within the coelomic cavity laterally and dorsally. Dorsally the circular muscle layer extends caudad to the end of the coelomic cavity and a short distance beyond, reaching approximately the posterior limit of the bases of the hind-limb buds. The circular muscle layer also becomes continuous posterior to the bladder anlage which is beyond the ventral limit of the coelomic cavity; but it does not extend as far into the extra-coelomic tissue ventrally as dorsally. Longitudinal muscles are not clearly distinguishable, and would thus seem to be less extensive than the circular layers.

A dorsal median ridge of the gut epithelium, extending from the urinogenital aperture to the anterior limit of the bases of the hind-limb buds, is present and constitutes a characteristic feature observable in adults, in which it extends to the cloacal aperture.

Figs. 5 and 6.

Ascaphus larva, Stage 51 (both figs. from one specimen). Cloacal region x 25.

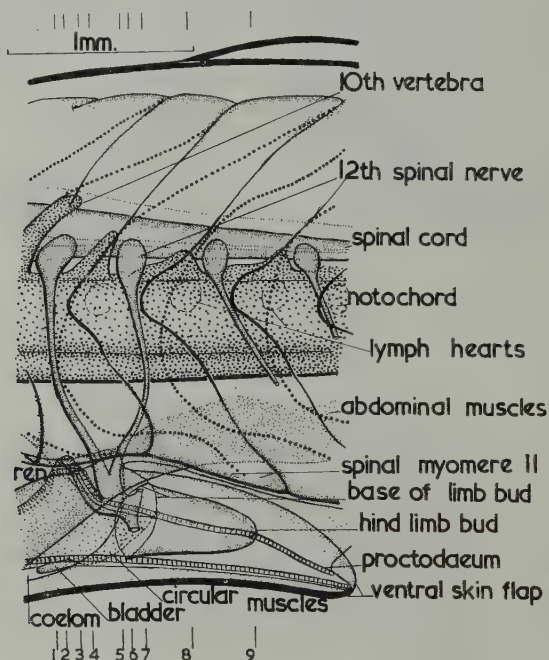


Fig. 5.

Norma lateralis sinistra.

Graphic reconstruction from transverse sections.

The plexus ischio-coccygeus, arising from nerves 9—12, passes to the hind-limb buds along the extreme posterior edge of the lateral wall of the coelom. The 10th spinal arch, but not the 11th, extends above the spinal cord.

The abdominal muscle cord of each side passes caudad and mediad under the spinal myomeres at the level of the posterodorsal limit of the coelom, and lies in contact with the medial face of the 11th spinal myomere and subsequent myomeres, its posterior limits not being distinct. A slight fold in the outer aspects of the 10th and 11th myomeres may be observed accommodating the abdominal muscle cord, which passes between these myomeres and the base of the hind-limb bud of that side.

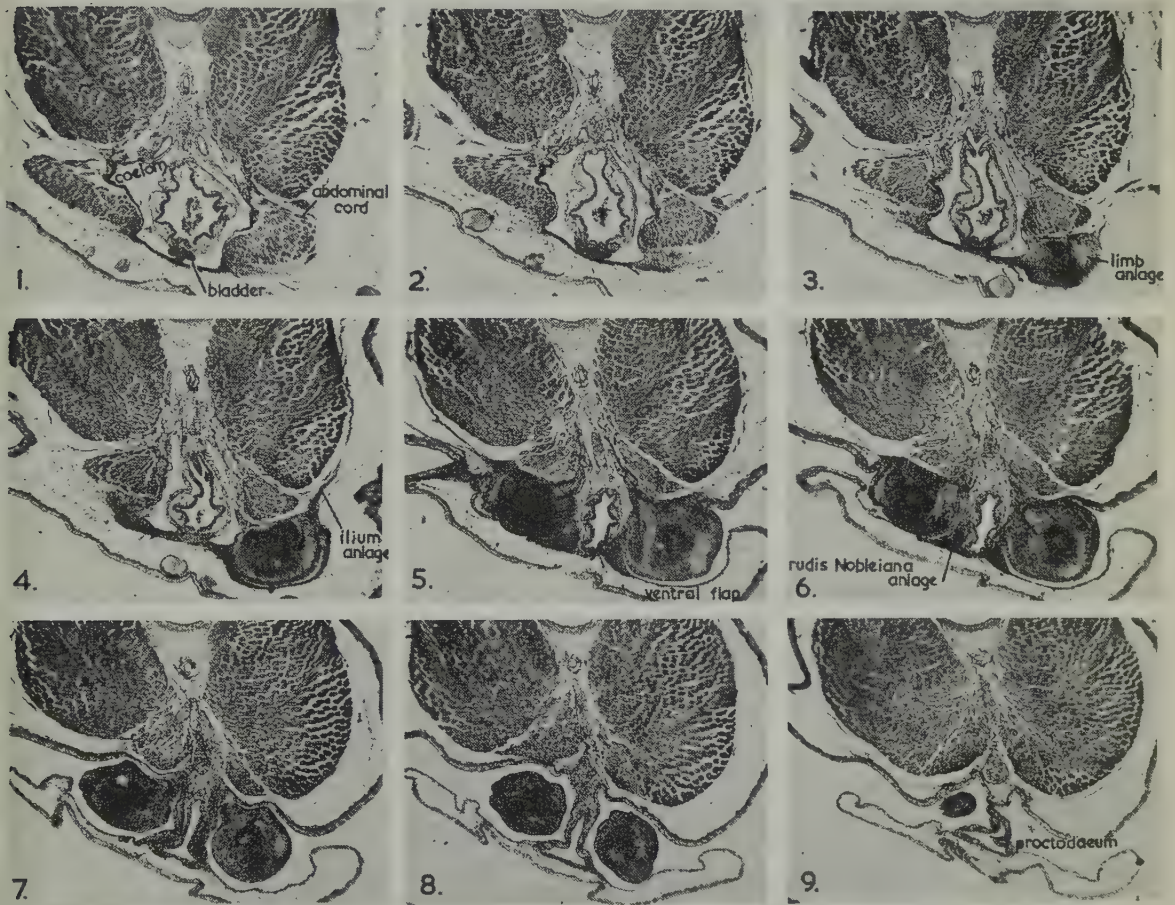


Fig. 6.

Norma posterioris. Photomicrographs of transverse sections.
(The numbers refer to levels in fig. 5.)

The kidneys and their ducts extend to the level of the 10th spinal myomere.

At the level of the urostyle 4 coccygeal lymph hearts are present laterally near the anterior edges of the 11th to 14th spinal myomeres.

At the ventral limits of the bases of the hind-limb buds, and along the medial borders of these bases, are thickenings; these ventrally representing the (post-pubic) rods of Noble, and dorsally the fibrous connective tissue which extends to the urostyle from the posterior tips of these rods in the adult, particularly the female adult.

The anlagen of the muscles of the hind limbs are becoming distinguishable around pro-cartilage in the limb-buds; the anlagen of the mm. pyriformes and mm. caudalipuboischiotibiales are indicated by extensions from the myogenic tissue of the limb-buds towards the urostyle.

Stage 52 (fig. 7)

At this stage the segmentation of the abdominal muscles can be made out in longitudinal sections. What is presumably the n. iliohypogastricus can be observed to innervate the second last of the series of abdominal segments near its posterior myocomma. Since the nerve is clearly derived from the 8th spinal nerve, this muscle segment can be identified as that corresponding to the 8th spinal myomere. The correspondence between the spinal myomeres and the abdominal myomeres may thus be plotted (broken lines in fig. 7). It is then evident that the abdominal segment corresponding to the 2nd spinal myomere is rudimentary and the one before it is absent.

The hind-limb bud is slightly shorter than the ventral flap of skin; the 10th vertebral arch is well developed.

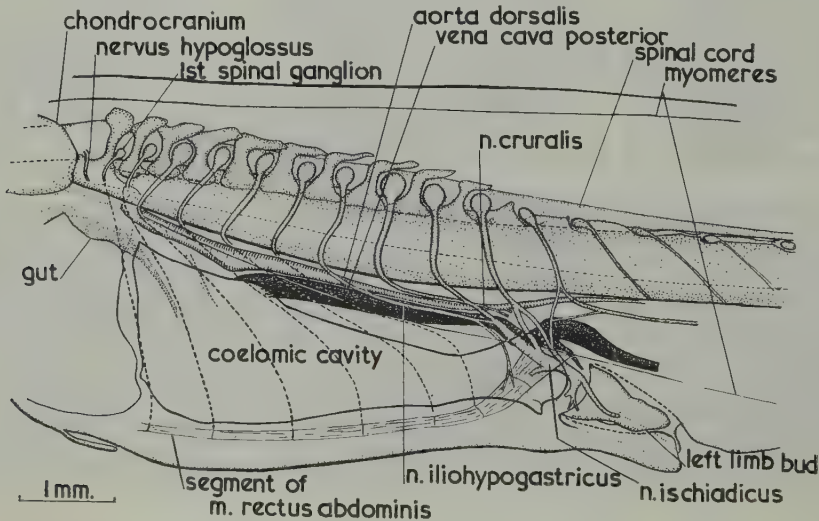


Fig. 7.

Ascapthus larva, Stage 52. Trunk region (norma lateralis sinistra) x 12.5
Graphic reconstruction from sagittal sections.

Stage 56 (figs. 8—10)

The proctodaeal aperture has the same form as in Stages 51 and 52, but is not as near to the tip of the ventral flap. The ventral projection from the tail attaching to the dorsal wall of the proctodaeum is notched so that its edge slopes cranioventrad then caudoventrad. The flap of skin and the proctodaeum are thus suspended more freely than in Stage 51. At the level of the bases of the hind-limbs the proctodaeum is more dorsal than further posteriorly, and there is a distinct slope between the two levels. The appearance of the proctodaeum at the slope is that of the more anterior part dorsally and of the more posterior part ventrally, this being particularly noticeable in the breadth of these portions — dorsally the proctodaeum narrows gradually caudad, ventrally it narrows more rapidly cephalad (fig. 9).

The bladder has separated from the urodaeum, and partially from the floor of the coelom, anteriorly. It is anteriorly notched medially and thus bluntly bifid. The lumen is distinct, anteriorly bifid and anterolaterally it projects dorsally. There is a distinct common portion of the nephric ducts which opens into a fairly easily distinguishable urinogenital sinus directly dorsal to the bladder.

The floor of the coelomic cavity is raised to the level of the bladder just anterior to the bases of the hind limbs. The coelomic cavity extends behind the bladder, and above its level, on either side of the gut, projecting more than half-way into the region of the bases of the hind limbs. As the plexus ischio-coccygeus is now also further forward, being situated approximately at the level of the nephric aperture, the coelomic cavity extends considerably posterior to the plexus. The coelomic cavity reaches the level of the 13th spinal ganglion posteriorly; dorsally it reaches about two fifths of the distance to the vertebral column medial to the spinal myomeres. As the coelom stretches further dorsally as well as posteriorly than in earlier stages, the abdominal muscle cord still passes across its posterodorsal limit.

The abdominal muscle cord of each side lies under the 10th spinal myomere, being internal to the 10th, 11th and 12th myomeres posteriorly and forming a broad ventral sheet, isolated from the spinal myomeres, anterior to the pelvic girdle. The ventral sheets are medially quite close to each other, the connective tissue between them constituting the *linea alba*. Signs of segmentation are slight in the ventral sheet, but posteriorly there are two distinct segments on each side. A nerve corresponding to the 8th spinal myomere, and a branch from the 9th spinal nerve, together form the nerve — hence presumably the *n. iliohypogastricus* — which supplies the abdominal segments on each side at the myocomma between the ventral sheet and the next segment. (The nerve corresponding to the 8th spinal myomere passes to the lateral surface of that myomere, traverses the lateral surface of the 9th spinal myomere, and meets the branch from the 9th spinal nerve ventral to the myomeres somewhat anterior to the ventrolateral edge of the 10th spinal myomere.) The nerve in the myocomma gives fibres to both the segment behind it and the broad ventral sheet in front of it, these therefore presumably corresponding to the 9th and 8th spinal myomeres respectively. The last segment of each side constitutes the portion on the inner faces of the spinal myomeres and presumably corresponds to the 10th spinal myomere. The

positions of the last two segments on each side is such that they could be considered posterior extensions of the corresponding spinal myomeres, as may be well seen in dorsal view (fig. 9).

The pelvic girdle is present in the form of two cartilages anterior to the bases of the hind limbs; the hind limbs are clearly divisible into femur, crus

Figs. 8—10.

Ascaphus larvae, Stage 56 (figs. 8 and 9 from one specimen). Pelvic region x 25.

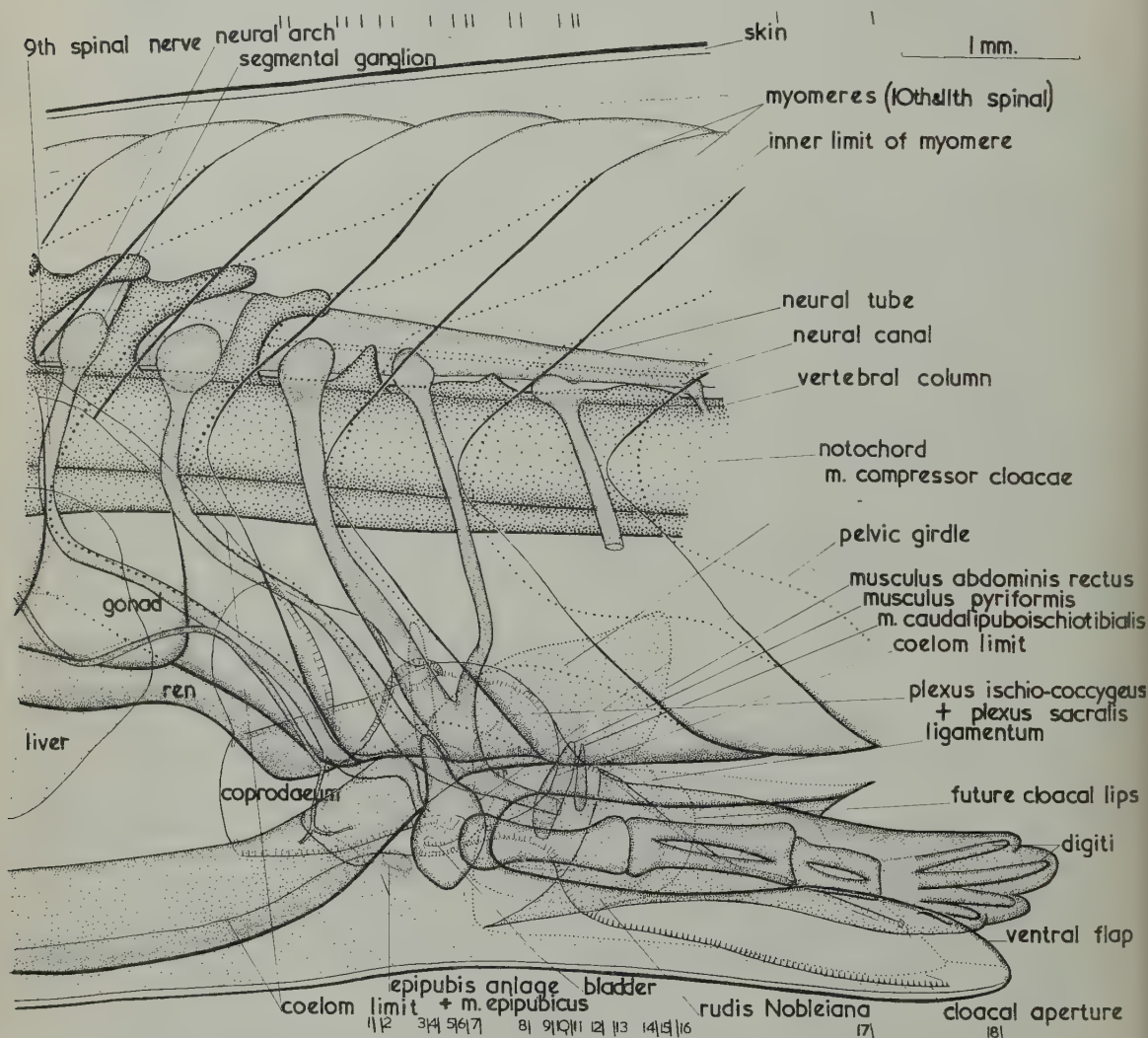


Fig. 8.

Norma lateralis sinistra. Graphic reconstruction from transverse sections.

and pes, each with its cartilaginous skeleton well differentiated. The position of the halves of the pelvic girdle and of the limbs indicates a forward and dorsal growth of the tissue at the bases of the hind-limb buds. This movement has resulted in the lifting of the coelom, proctodaeum and urodaeum in the pelvic region.

Anterior to the pelvic halves, at the medial edges of the myocommata between the ventral abdominal muscle sheets and the following segments, the anlagen of the epipubes (or halves of the epipubis) are visible as condensations of cells in the connective tissue stretching from these myocommata to the

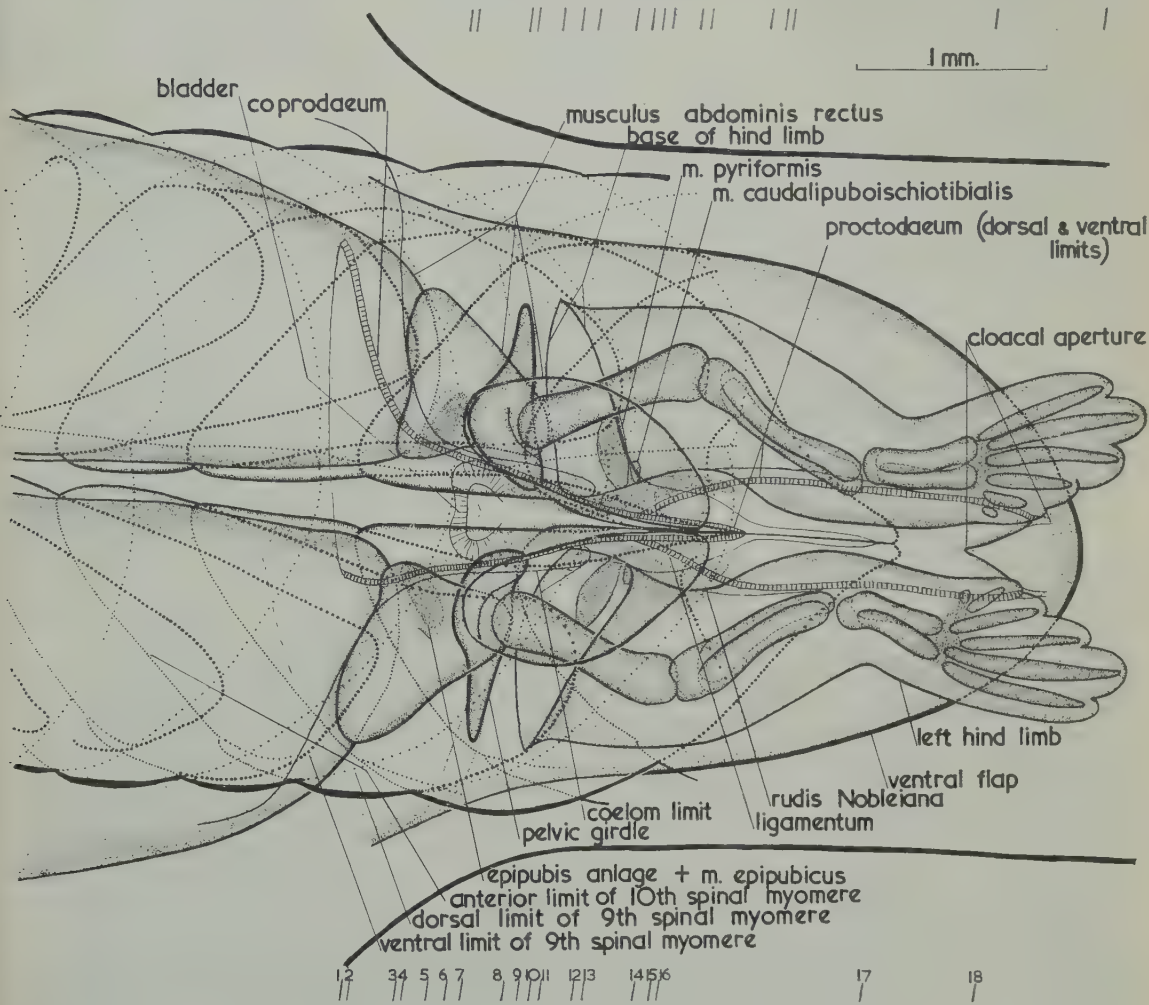


Fig. 9.
Norma dorsalis. Graphic reconstruction from transverse sections.

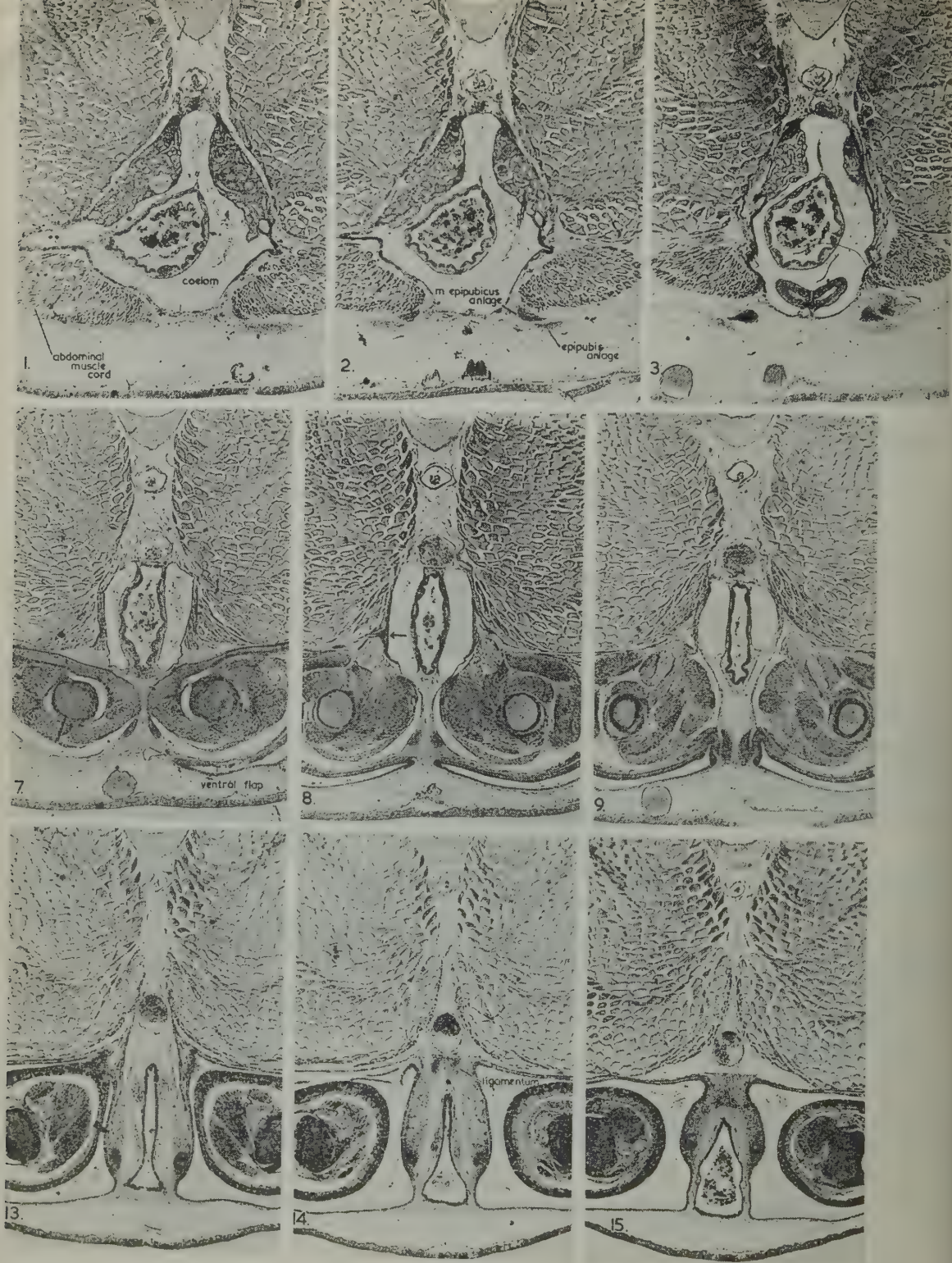
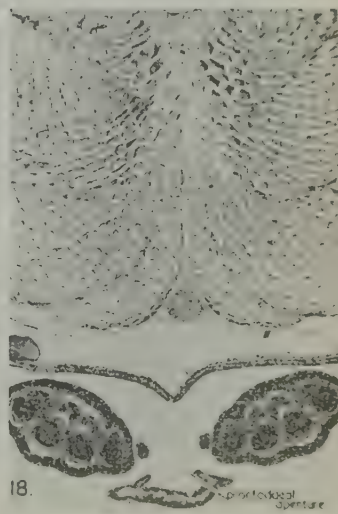
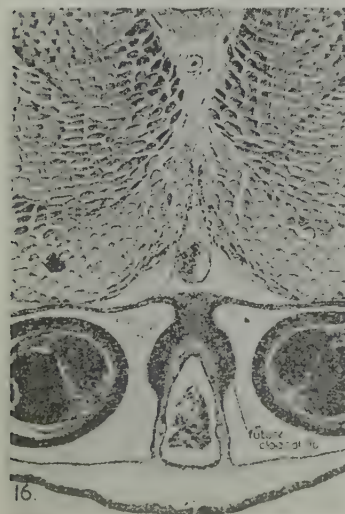
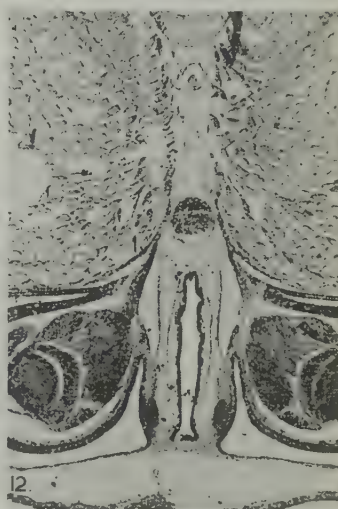
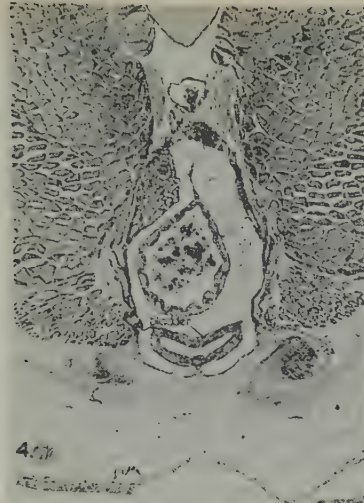


Fig. 10.
 Norma posterioris. Photomicrographs of transverse sections (female specimen).
 (The numbers refer to corresponding levels in figs. 8 and 9.)
 An arrow in the figure at level 10 indicates the m. circumflexor arteriae.



pelvic halves. Dorsal to the epipubic anlagen, and considerably more distinct, are the mm. epipubici.

An aggregation of cells continues posteriorly from the epipubic anlage of each side medioventral to the pelvic girdle half, becoming the (post-pubic) rod of Noble posteriorly. These rods thus begin anteriorly medioventral to the posterior third of the pelvic girdle. Behind the pelvic girdle the rods of the two sides approach each other beneath the proctodaeum, parting again as the proctodaeum slopes posteroventrally between them and turning medio-dorsally at their posterior tips. The rods extend about two thirds of the way across the sides of the sloping portion of the proctodaeum. At their posterior tips the rods approach not only each other in the horizontal plane, but also a similar aggregation of cells forming a ligament which lies dorsal to the cloaca. From the anterior tips of the rods dense connective tissue stretches medial to the pelvic girdle halves dorsally.

In the region of the tips of the rods of Noble the skin laterodorsal to the proctodaeum is thicker than further posteriorly, these thicker walls representing the future cloacal lips. The median dorsal ridge of the urodaeum and proctodaeum is absent posterior to this point, but it is distinct somewhat anterior to it.

Near the posterior end of the bases of the hind limbs the mm. caudalipuboischiotibiales are located, lying dorsomedial-lateroventrally on either side of the dorsal half of the proctodaeum. Just anterior to the mm. caudalipuboischiotibiales the mm. pyriformes have their origins at the same horizontal and lateral levels. Their direction is more lateral than that of the former muscles, and they are longer, since they reach to the femurs. The mm. pyriformes just reach the level of the coelomic cavity anteriorly.

The mm. compressores cloacae have developed, stretching across the medial faces of the posterior segments of the abdominal muscles dorsally and passing on either side of the gut ventrally to approach the dorsal surfaces of the rods of Noble. Posteriorly the mm. pyriformes and the mm. caudalipuboischiotibiales lie between the mm. compressores cloacae and the abdominal muscles. Anteriorly the mm. compressores cloacae end some distance from the rods of Noble, further posteriorly they attach to the rods. Just posterior to the hind-limb bases the mm. compressores cloacae become indistinct. Posterior to the bladder the mm. compressores cloacae become continuous ventrally in the pelvic girdle region. Anteriorly slips of muscle continuous with the mm. compressores cloacae extend anterolaterally, a dorsal slip stretching along the lower half of the medial faces of the posterior abdominal segment of each side and a ventral slip curving around the arteria ischiadica and the nervus ischiadicus at the point at which the artery twists caudolaterad over the nerve. The ventral slip of muscle is here named m. circumflexor arteriae to facilitate reference.

The circular muscle layer of the gut can be detected approximately as far posteriorly as the mm. compressores cloacae, but it is incomplete ventrally posterior to the coelom. Posterior to the coelom there are few indications of a longitudinal muscle layer. Just posterior to the pelvic girdle, and to the ventrally complete mm. compressores cloacae, there are two cords of longitudinal muscle ventral to the gut. Indications of longitudinal muscle are also visible dorsolateral to the gut at this level.

The lymph sacs of the limbs have developed and extend from the hind-limb bases ventrally, and medially both cephalad and caudad, dorsal to the rods of Noble. The rods of Noble are firmly adherent to the ventral flap of skin posteriorly; anterior to the bases of the hind limbs there are small lymph spaces ventral to the rods separating them partially from the ventral skin.

Veins on either side of the proctodaeum just anterior to the future cloacal lips drain considerable sinuses around the proctodaeum in this region.

The gonads have developed, and the sex of some specimens may be determined at this stage.

Stage 58, Male (figs. 11 and 12)

The proctodaeum has become considerably shorter by loss of the greater proportion of that part which was associated with the ventral flap of skin, the latter being greatly reduced in length and breadth while the skin which suspended it from the tail region is entirely absent. The proctodaeal aperture is now at the end of the downward-sloping portion behind the pelvic girdle. The median dorsal ridge of the gut epithelium now extends to the proctodaeal aperture, and the (post-pubic) rods of Noble, dorsal ligament, mm. compressores cloacae, and circular muscle layer, reach to a point dorsal to the posterior limit of the proctodaeal aperture; the rods of Noble, in extending dorsal to the proctodaeum, completely surround it laterally. A rudimentary "tail" is formed by these structures, little change in relative positions having taken place in its formation. The dorsal ligament is now much more distinct and projects dorsally at the level of the posterior limit of the fold between the thigh and the cloacal extension ("tail"), splitting to pass on either side of the caudal vein.

The approximation of the halves of the pelvis lifts the proctodaeum and urodæum to the level of the ilia, so that the slope of the proctodaeum behind the pelvic girdle is much steeper than in earlier stages. As the process of approximation begins posteriorly and extends forward, the urodæum and bladder are forced somewhat further forward, as they are lifted. Enlargement of the halves of the pelvic girdle posteriorly results in the ischial regions reaching the anterior edges of the ventral ends of the mm. pyriformes and thus almost to the posterior end of the coelom, the relations between coelom and mm. pyriformes having undergone little change. The halves of the pelvic girdle are separated only by a thin layer of dense connective tissue in the ischial region, anteriorly the halves are still well separated.

The bladder extends from the posterior edge of the ilium to a level in front of the pelvic girdle. It is bifid and well separated from the coprodæum, on either side of which it projects anteriorly.

The floor of the coelom lifts steeply from in front of the pelvic girdle to a position between the ilia, but the posterior and dorsal limits are little changed.

The relation of the abdominal muscle cord to the coelom and the pelvic girdle is little altered; the increasing height of the body in this region, however, causes the muscles to assume an almost vertical position. At the same time degeneration of the posterior segments has taken place so that the dorsal portion of the cord is scarcely distinguishable. Close to the degenerating

segments on each side the m. transversus and m. obliquus have differentiated. On the ventral surfaces of the ventral muscle sheets the presence of smaller, more basophilic, fibres reveals the differentiation of secondary muscles — the superficialis layer of the rectus abdominis muscles. The dorsal degenerating portion of each abdominal muscle cord is associated with the 10th and 11th spinal myomeres of the corresponding side, but somewhat more anterior regions of these spinal myomeres than before. This is clearly shown by the relations to the nephric ducts, which open at a level between these degenerating muscles.

The mm. compressores cloacae extend to the tips of the rods of Noble posteriorly and attach to them ventrally as far forward as just behind the pelvic girdle. Further anteriorly the two muscles approach each other

Figs. 11 and 12.

Ascaphus larva, Stage 58, male (both figs. from one specimen).

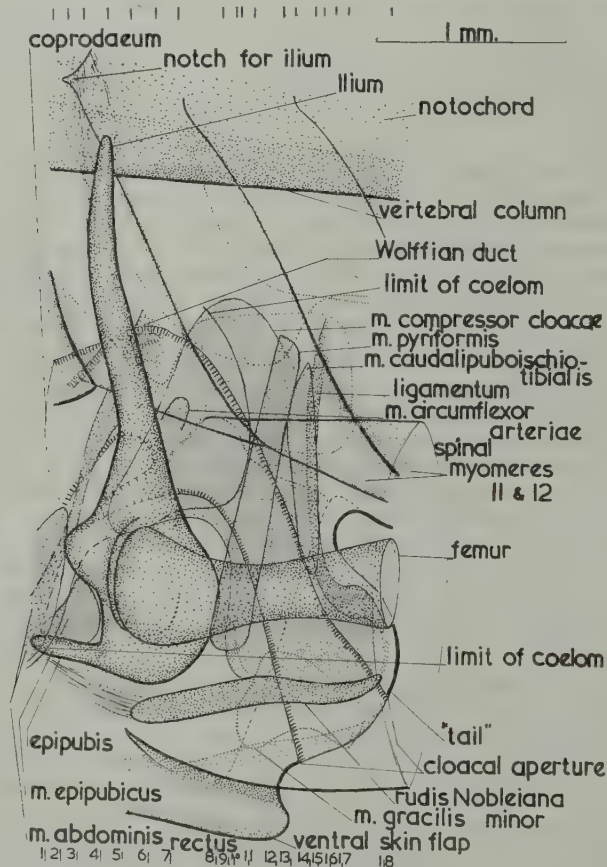


Fig. 11

Norma lateralis sinistra.

Graphic reconstruction from transverse sections.

ventrally, and, dorsal to the pelvic girdle, are again separate at their anterior limits, attaching to the pelvic girdle between the ilia. Dorsally the muscles extend to the ligament, which is the dorsal equivalent of the rods of Noble, posteriorly. Anterior to the ligament — which curves caudad dorsally — the mm. compressores cloacae extend further dorsal on the medial faces of spinal myomeres 10, 11 and 12, and are no longer separated from these by the abdominal muscle cords, as the latter have withdrawn just cephalad a little posterior to the ilia. The dorsal anterior slips of the mm. compressores cloacae, which were associated with the abdominal muscle cords, are not distinguishable, while the ventral anterior slips are quite distinct, here being designated (see previous stage) as mm. circumflexores arteriarum because they curl around the arteriae ischiadicae. The anteroventral tips of the mm. compressores cloacae lie considerably further forward, extending more than half-way across the pelvic girdle and well beyond the opening of the bladder. Relations to the coelom posteriorly indicate relatively little extension of the muscles posterodorsally.

The mm. compressores cloacae and the mm. graciles minores are closely associated, the former attaching to the dorsal surfaces of the rods of Noble at the same level as that at which the latter originate laterally from them.

The mm. pyriformes and mm. caudalipuboischiotibiales have extended both ventrally and dorsally without changing their antero-posterior relations to any extent. The mm. pyriformes reach to the ventral surfaces of the femurs and both pairs of muscles extend dorsally further than the mm. compressores cloacae, being associated with the medial faces of the 10th spinal myomeres — which are curved mediad in this region.

The ilia have shifted slightly forward relative to the lateral surfaces of the 10th spinal myomeres, extending on each side from the anterior half of the myomere ventrally towards a notch on the posterior margin of the myomere. Dense connective tissue, in the form of strands, extends from the tips of the ilia into the myocommata between the 10th and 11th spinal myomeres at the notches. The tips of the ilia reach half-way up the hypochorda of the vertebral column.

The epipubic cartilages are well developed and are continuous with the pubic region of the pelvic girdle halves, but not with each other. The mm. epipubici extend from the anterior faces of the halves of the pelvic girdle and attach to the dorsal faces of the epipubic halves. From each half of the epipubis there is a dense connective tissue connexion with the rods of Noble which passes ventromedial to the halves of the pelvic girdle. Anteriorly the m. rectus abdominis of each side is attached to the epipubic cartilage.

The m. pectineus of each side extends forward dorsal to the m. epipubicus of that side, anteriorly curving somewhat medioventrally towards the epipubis, but not attaching to it.

The rods of Noble have been ventrally displaced anteriorly by the approximation of the halves of the pelvic girdle above them, and this has caused some inflected curvature anterior to the proctodaeum, the rods now having an elongated-S shape. The dorsal ligament lies in a narrow septum between the lymph sacs at the bases of the hind limbs, the septum therefore being the septum interfemorale between the sacci interfemorales.

The skin of the "tail" is beginning to separate from the proctodaeum

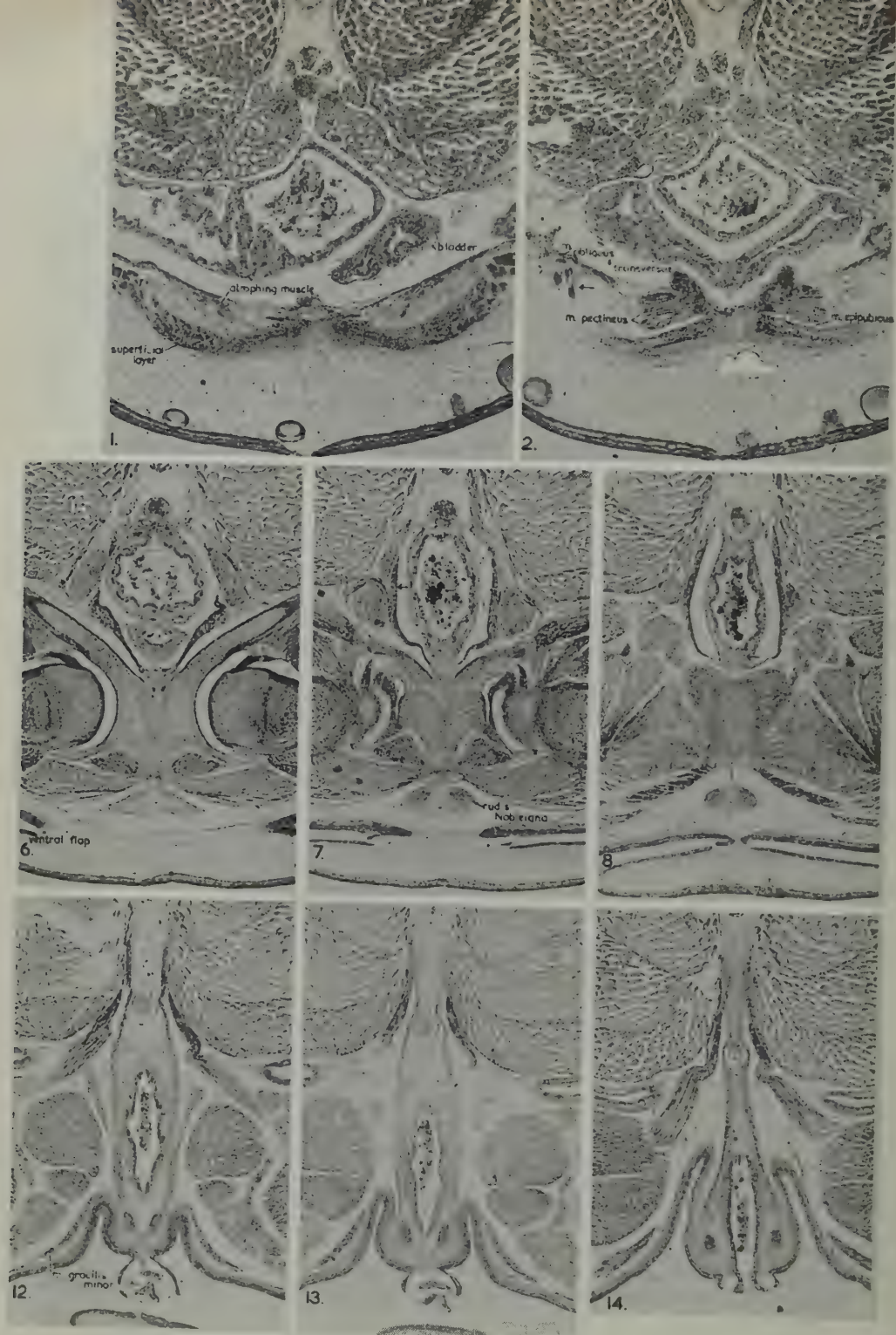
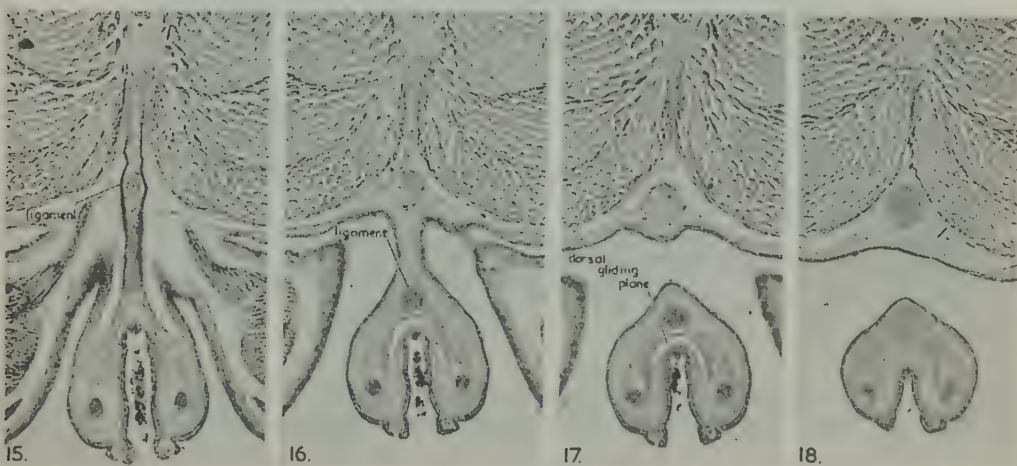
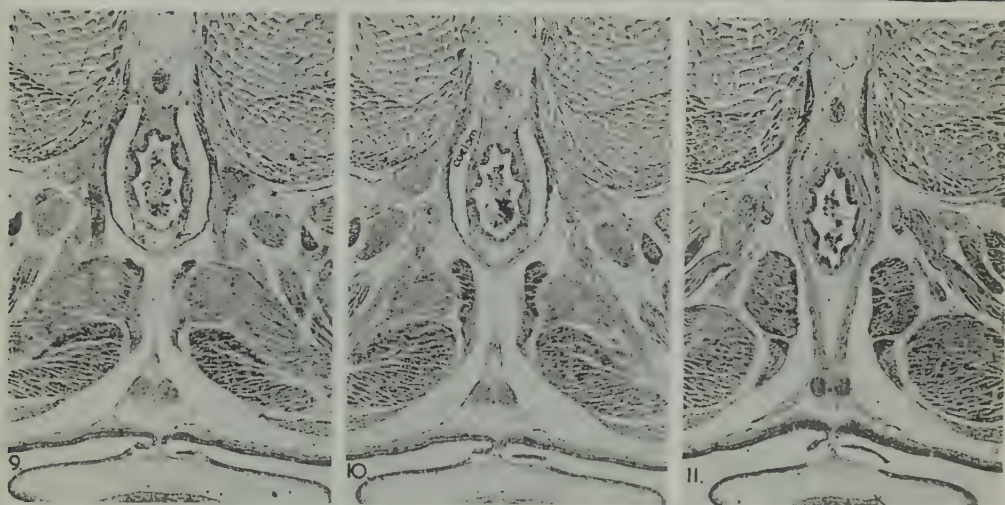
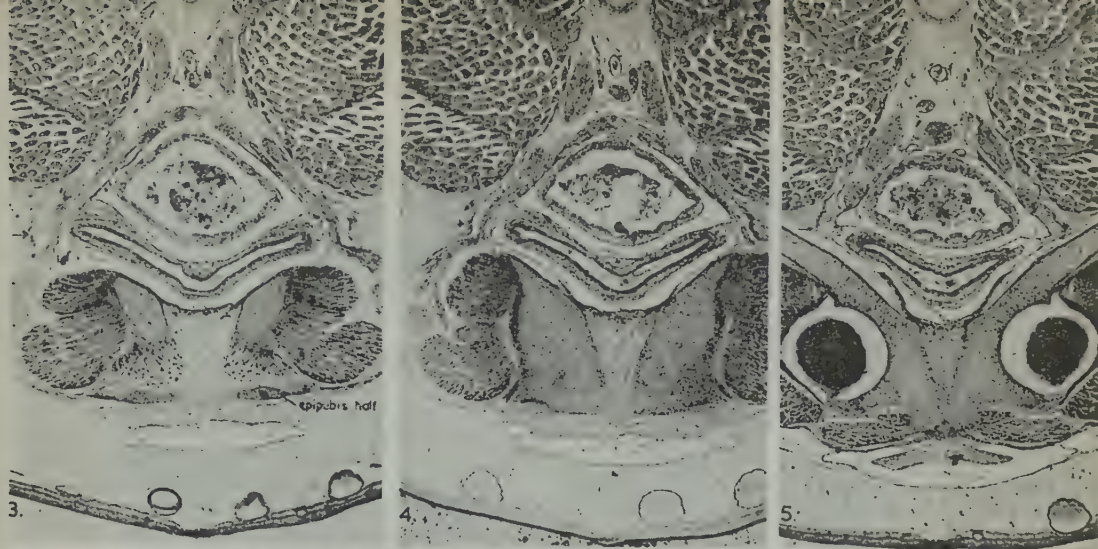


Fig. 12.

Norma posterioris. Photomicrographs of transverse sections. Arrows in the figure at levels 2—6 indicate the atrophying abdominal muscle cord, and at level 7 indicate the m. compressor cloacae and the m. circumflexor arteriae.



dorsally and dorsolaterally at the bases of the hind limbs, the lymph spaces produced being in communication with the sacci interfemorales, which extend a short way distally along the femurs. The dorsal gliding plane of the cloacal extension ("tail") has also developed.

The increase in the lymph spaces around the proctodaeum has left the

blood vessels and the nerves (12th) of this structure suspended between the posteromedial edges of the mm. pyriformes and the dorsolateral edges of the mm. compressores cloacae in the cloacal extension.

Stage 60, Male (figs. 13, 14 and 15)

Figs. 13—15.

Ascaphus larva, Stage 60, male (all figs. from one specimen).

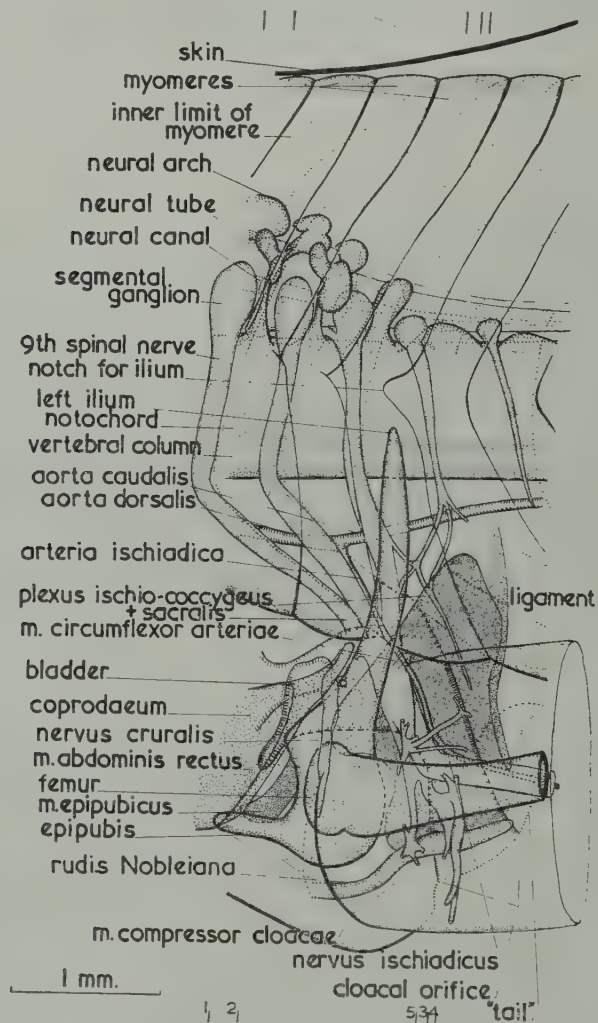


Fig. 13.

Pelvic region (norma lateralis sinistra).
Graphic reconstruction from transverse sections.

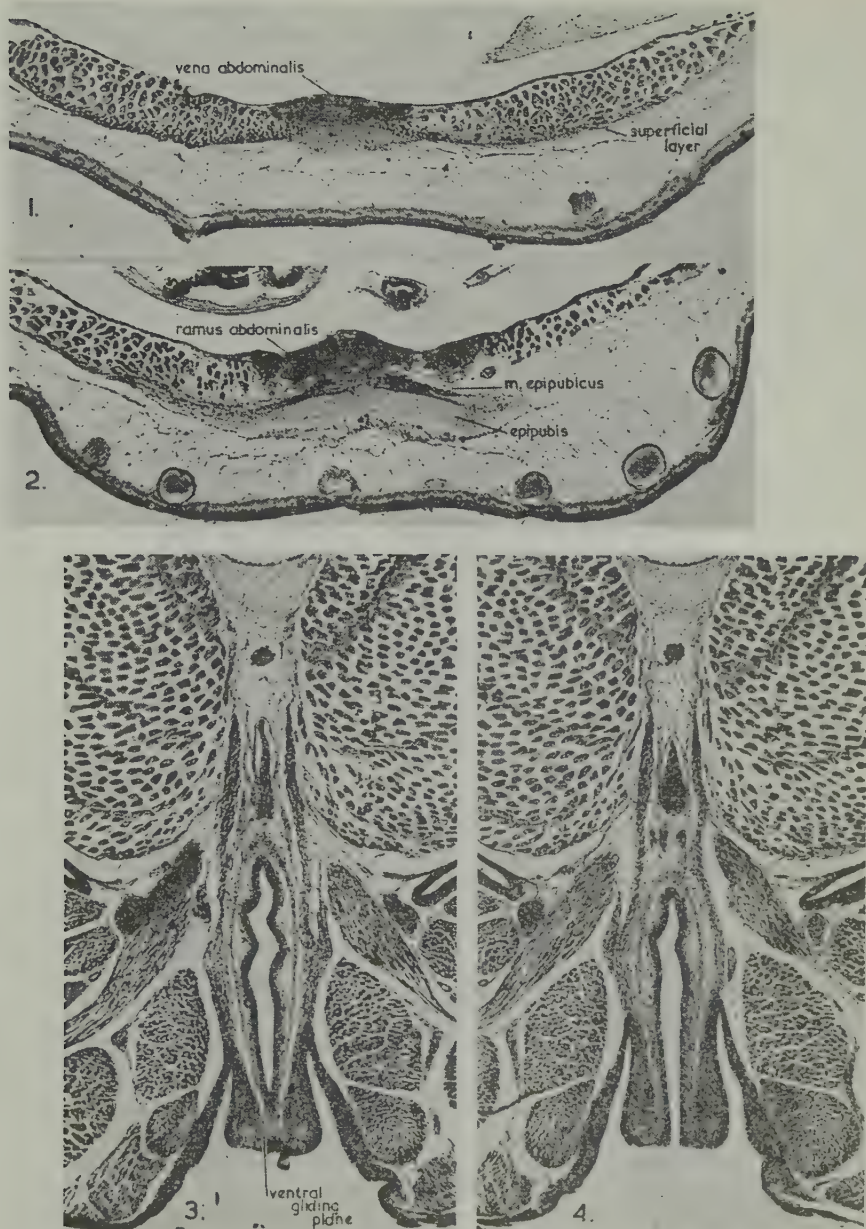


Fig. 14.

Epipubic and proctodaeal regions (norma posterioris) $\times 25$.
Photomicrographs of transverse sections. (The numbers refer to levels in fig. 13.)

The ventral flap is further reduced both in length and breadth. The proctodaeal orifice has a somewhat more dorsal position.

The abdominal cords are not easily traceable on the medial faces of the spinal myomeres, the posterior segment apparently having disappeared. Ventral to the spinal myomeres two segments associated with the epipubis can be made out on each side, the anterior of these being part of the *m. abdominis rectus*. The more posterior and dorsal segment on each side is closely associated with the *m. iliacus internus*, being separated dorsally from this muscle only by *n. cruralis*, while ventrally it is associated with the *m. pectineus*. The *m. abdominis rectus superficialis* is well developed.

The two halves of the epipubis are fused anteriorly, enclosing a considerable space between themselves and the pelvic girdle. The two halves of the pelvic girdle have fused posteriorly.

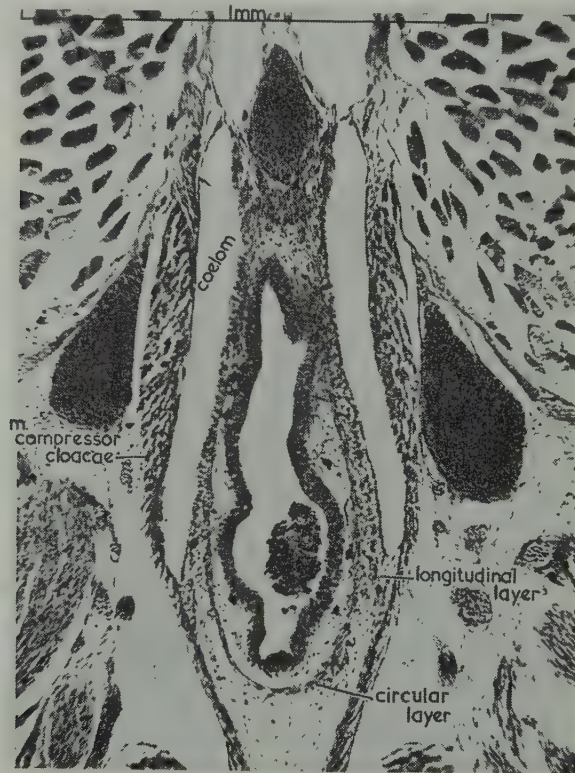


Fig. 15.
Region of the posterior limit of the coelom
(norma posterioris) x 50.
Photomicrographs of transverse section.
(The level of the section is indicated by 5 in
fig. 13.)

With the formation of a vena abdominalis (showing signs of a dual origin) dorsal to the anterior tip of the epipubis and to the linea alba further anteriorly, the vascular system in the pelvic region has attained essentially the adult form.

Anterior to the ventral lip of the proctodaeal orifice a ventral gliding plane has developed; it is incomplete midventrally.

Stage 62—63, Male (figs. 16 and 17)

The proctodaeal aperture is somewhat more dorsal, particularly its upper rim, and there is a more marked fold between the cloacal extension ("tail") and the tail. The mm. compressores cloacae now reach further dorsally, to beyond the aorta caudalis, and are separated from each ventrolateral edge of the vertebral column by a short tendinous band only. Anteriorly the mm. compressores cloacae have shifted forward to a position lateral to the urino-genital aperture. The mm. circumflexores arteriarum arising from the mm. compressores cloacae project beyond the anterior edges of the latter, the change in position being made possible by greater separation distally of the two muscles on each side. There is a forward shift of the plexus sacralis relative to the ilium.

The ilium now projects somewhat anterodorsally instead of postero-dorsally or vertically upwards from the acetabulum. This change is associated with a shift of the ilium posteriorly relative to the ventrolateral face of the 10th spinal myomere, while the dorsal tip of the ilium enters the notch at the posterior edge of the myomere, which notch is now deeper and hence extends further anterior. The tip of the ilium approaches the transverse process of the 10th, the sacral, vertebra, which lies lateral to, but not in contact with, the arch of the vertebra. The secondary muscles associated with the transverse process are well-developed.

The abdominal muscle cord is represented by the m. abdominis rectus originating on the epipubis. The epipubis is connected to the rods of Noble by a tendinous sheet of connective tissue which has two thickened portions revealing its paired origin.

Posteriorly the rods of Noble are distinctly continuous with the dorsal ligament, which now reaches to the vertebral column. Associated with the rods of Noble cavernous tissue has begun to develop; this tissue surrounds the rods behind the pelvis and also lies lateroventral and medioventral to the rods in this region. The mm. compressores cloacae have the same transverse niveau with the rods as has the cavernous tissue. Between the rods just anterior to the ventral rim of the cloacal orifice there are fibres of the mm. compressores cloacae. These are well isolated from differentiated circular and longitudinal muscle layers.

There is a urodaeal diverticulum where the common nephric duct opens into the urodaeum. The wall of the urodaeum and proctodaeum is little folded in comparison with the other larvae, and there is no median dorsal ridge. Just within the proctodaeal aperture, and cephalad, cloacal glands have begun to develop anteriorly. They are visible as thickenings in the epithelium.

Ventrally the cloacal extension, rods of Noble and mm. graciles minores have separated from the skin except just anterior to the proctodaeal aperture.

Figs. 16 and 17.

Ascapus larva, Stage 62—63, male (both figs. from one specimen).

Pelvic and cloacal regions x 25.

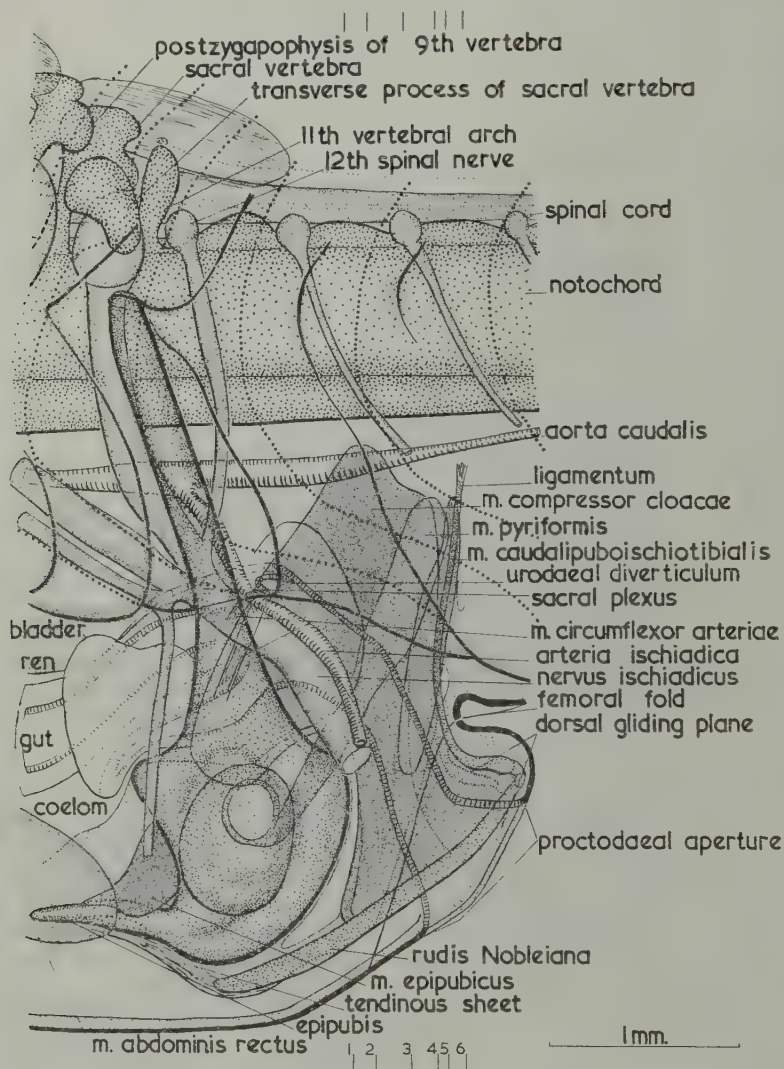


Fig. 16.

Norma lateralis sinistra.

Graphic reconstruction from transverse sections.

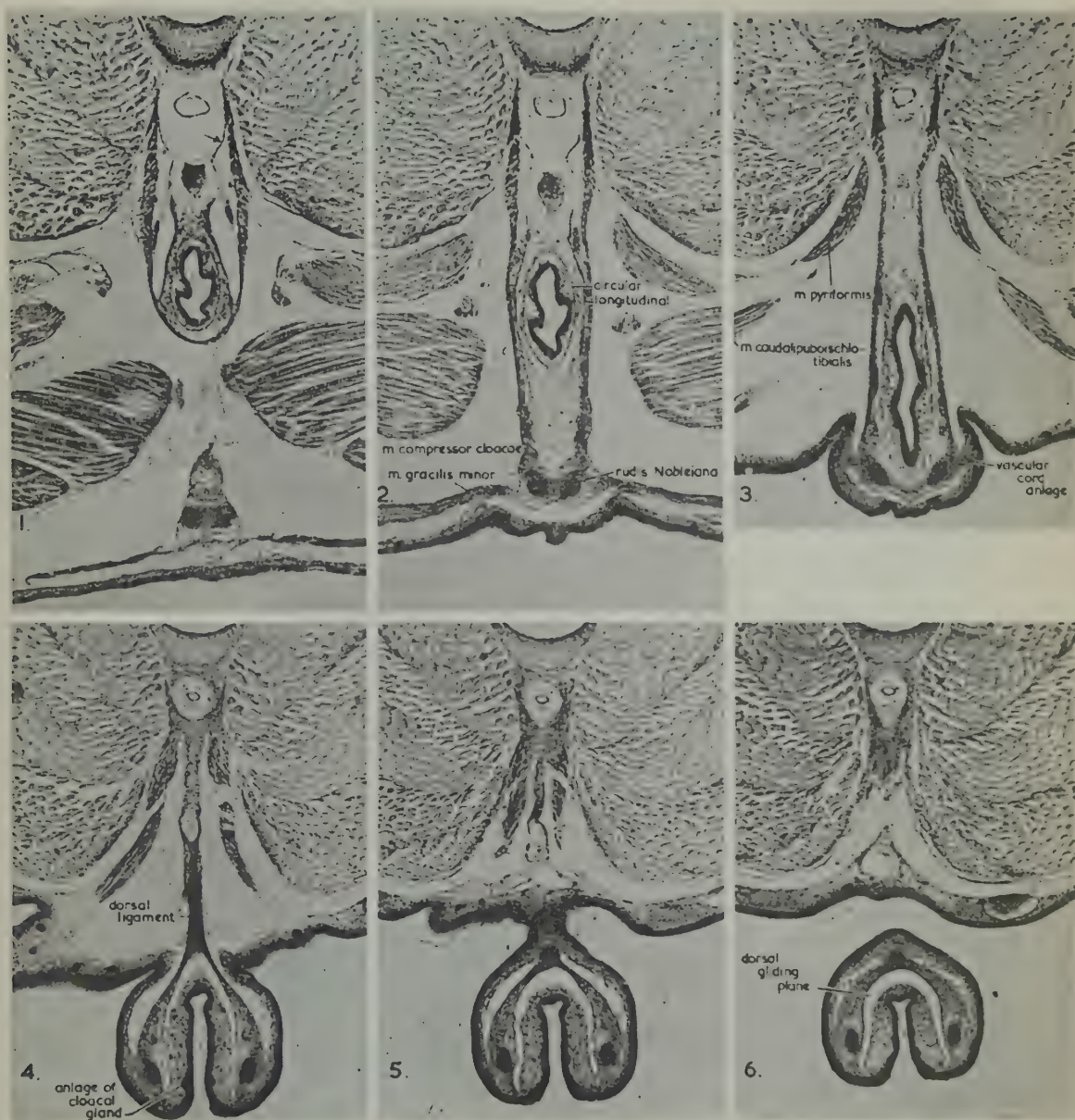


Fig. 17.

Norma posterioris (cloacal region). Photomicrographs of transverse sections. (The numbers refer to levels in fig. 16.)

The arrow in the figure at level 1 indicates the longitudinal muscle cord extending towards the vertebral column.

Stage 63, Female (figs. 18 and 19)

The fold between the tail and the cloacal extension has become still deeper. Cloacal glands are present in the ventral cloacal wall.

The mm. compressores cloacae maintain practically the same relations,

Figs. 18 and 19.

Ascaphus larva, Stage 63, female (both figs. from one specimen).
Pelvic region x 25.

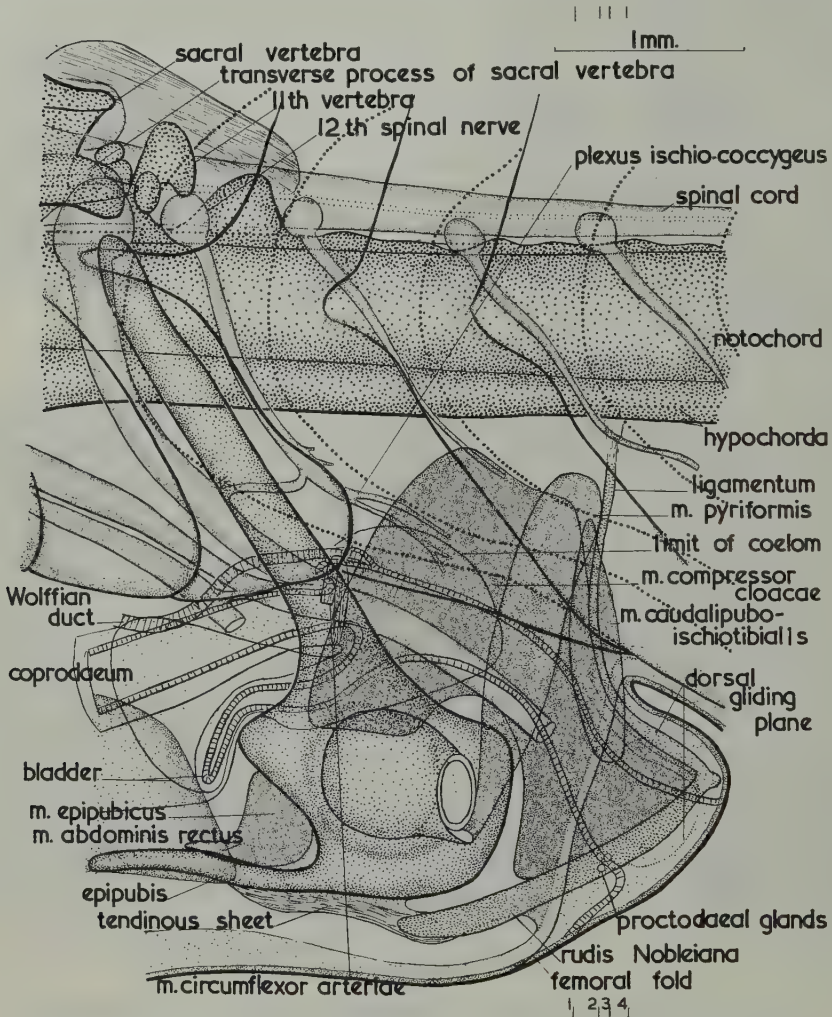


Fig. 18.

Norma lateralis sinistra. Graphic reconstruction from transverse sections.

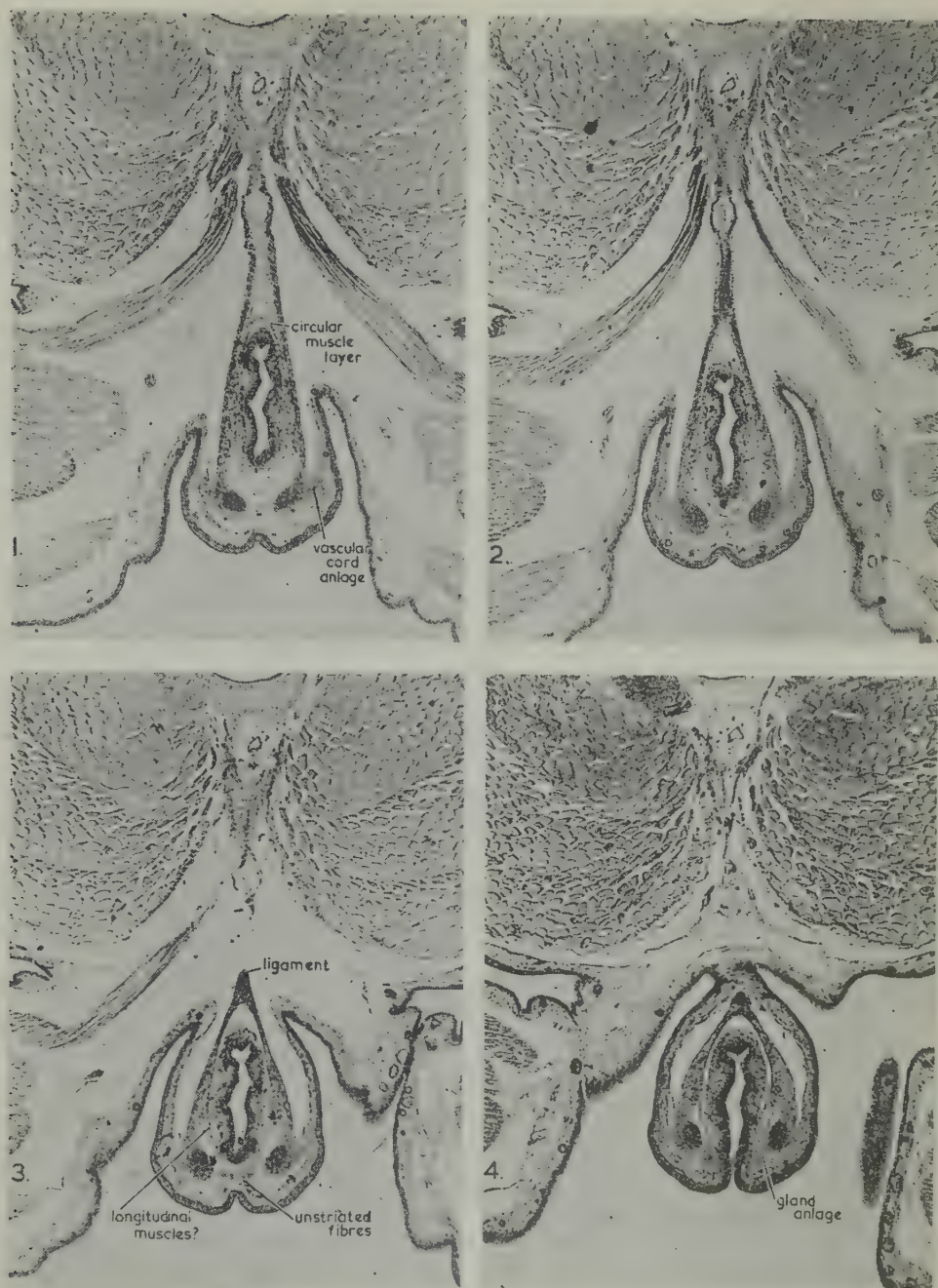


Fig. 19.
Norma posterioris. Photomicrographs of transverse sections.
(The numbers indicate levels in fig. 18.)

but in doing so have considerably lengthened antero-posteriorly, since the ischial region has become considerably larger. The origins of the mm. pyriformes are only slightly posterior to the ischia, and slightly posterior to a point at which the hypochorda becomes dorso-ventrally thinner.

On each side the dorsal portion of the ilium projects much more anteriorly, passing from a position lateral to the posterior extremity of the lateral face of the 10th spinal myomere to penetrate the very deep notch at the posterior margin of this myomere. It closely approaches the transverse process, now fused to the sacral vertebra. The plexus sacralis is displaced further anteriorly relative to the ilium.

The 12th neural arch reaches almost to the top of the spinal cord. The hypochorda is considerably smaller posterior to a point just behind the ganglion of the 14th spinal nerve than further anteriorly.

There is little change in the epipubis, tendinous sheet, rods of Noble, and dorsal ligament. Between the rods of Noble just anterior to the proctodaeal glands is a portion of the mm. compressores cloacae. The relation of this portion of muscle to the circular muscle layer is not clear.

Stage 64, Female (figs. 20 and 21)

The tail myomeres are considerably shorter dorso-ventrally, the ventral portions having been reduced. The proctodaeal aperture is considerably further dorsal, particularly its upper rim. The proctodaeal region has enlarged considerably so that the dorsal ligament is anterodorsally directed, instead of first being directed dorsally then curving posterodorsally nearer the vertebral column. This enlargement of the proctodaeum is partly due to the decrease of the tail, which is also more widely separated from the cloacal extension, providing more space for the proctodaeum. Cloacal glands are now distinct on the lateral walls of the cloaca.

The rods of Noble are longer and more sigmoid, the shape in the adult female being quite similar.

The mm. pyriformes and mm. caudalipuboischiotibiales are now close to the vertebral column and the former are dorsal to the ischia. The hypochorda has become thinner posteriorly from a point just in front of the level of the ganglion of the 14th spinal nerve (see previous stage), and it is at this point that the mm. pyriformes approach the vertebral column most closely.

The anterior edges of the mm. compressores cloacae have advanced further anteriorly. Since this is particularly so dorsally, the anterior edges are now nearly vertical. The plexus sacralis is relatively further cephalad and the ilium projects somewhat more anteriorly.

The mm. compressores cloacae are well developed in the region between the rods of Noble. The isolation of their fibres from the circular and longitudinal muscle layers is considerable in this region. Near the posterior end of the pelvic girdle the longitudinal muscles of the gut attach to the girdle ventral to these muscles and approach the urostyle dorsal to them (cf. also figs. 22 and 23). Behind the pelvic girdle they do not extend far as well-differentiated entities.

The 12th neural arch reaches the level of the top of the spinal cord at this stage.

Figs. 20 and 21.

Ascaphus larva, Stage 64, female (both figs. from one specimen).
Pelvic region x 25.

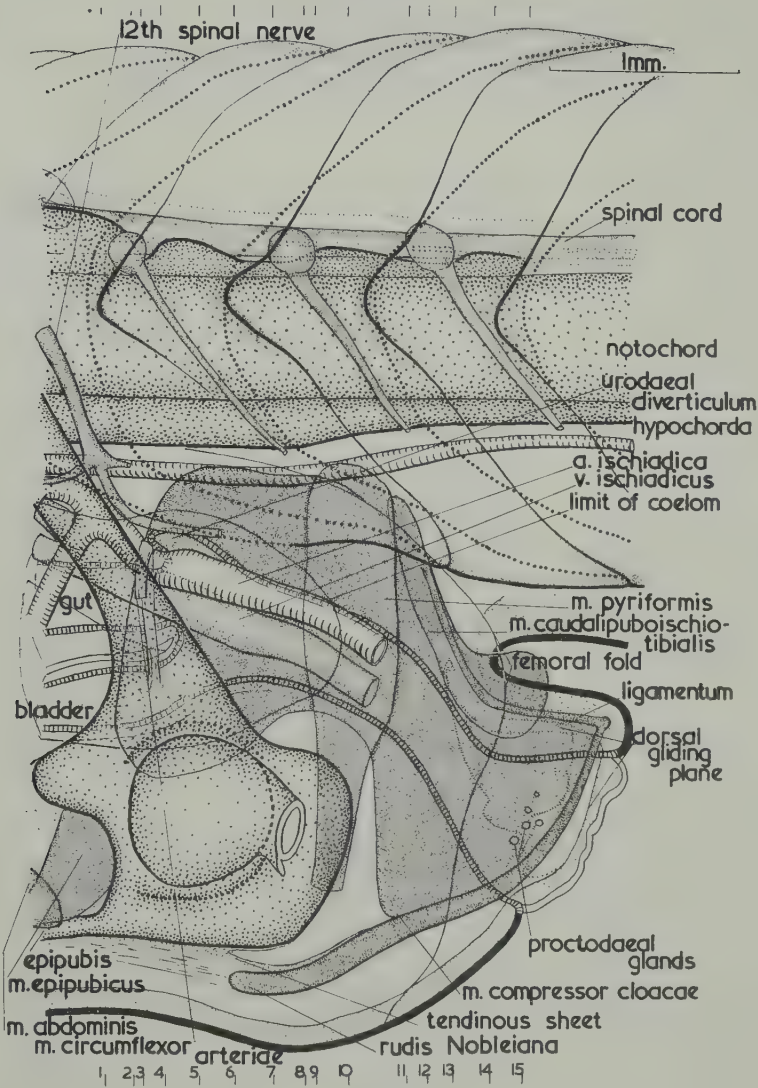


Fig. 20.

Norma lateralis sinistra.

Graphic reconstruction from transverse sections.

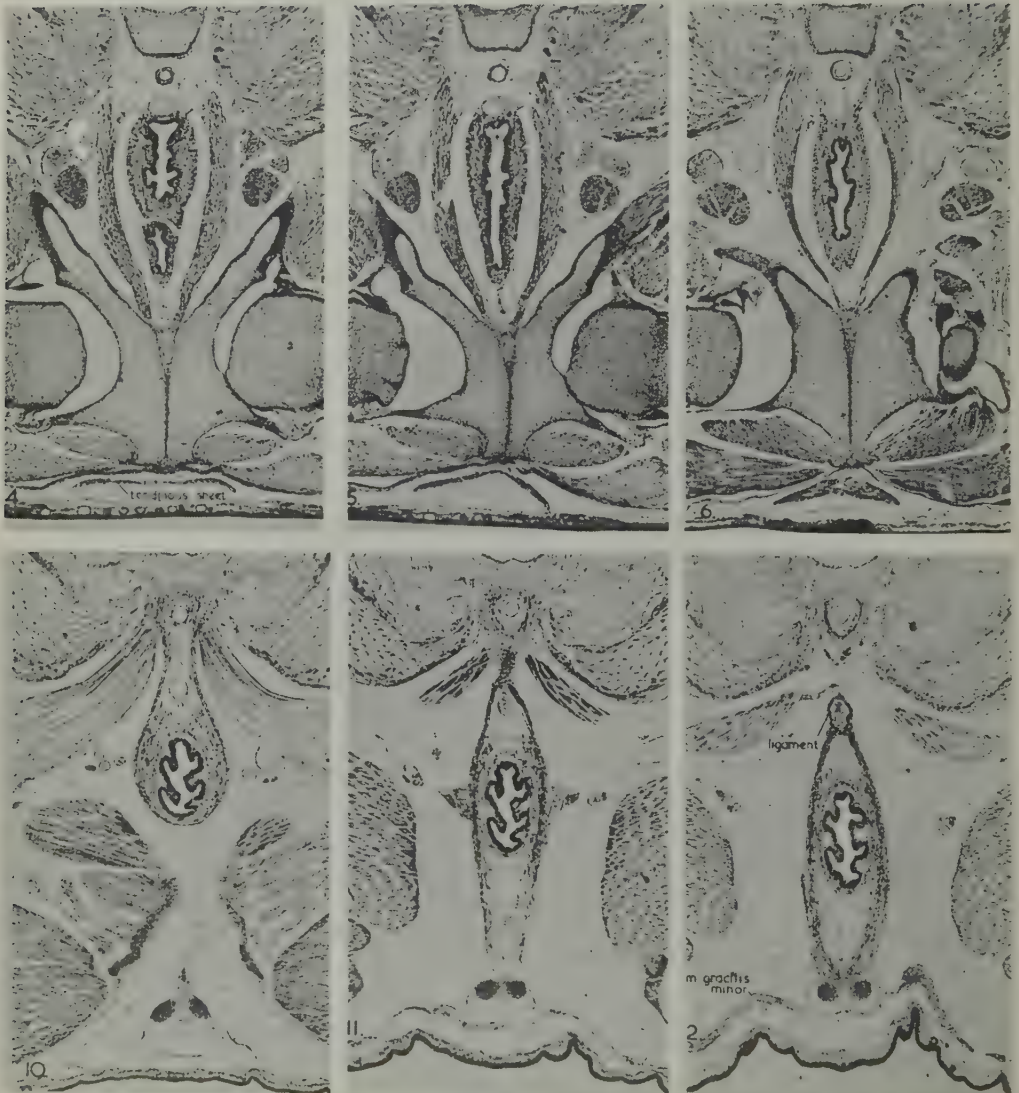
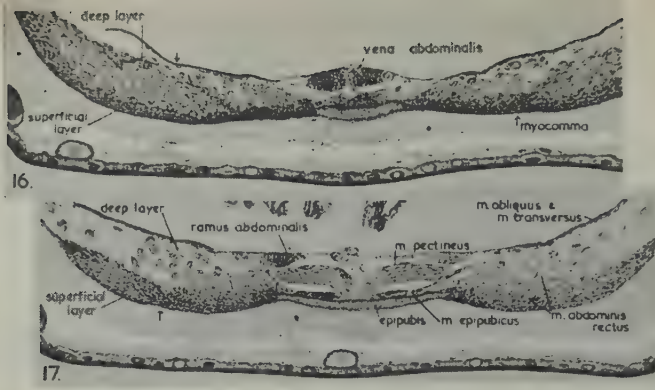
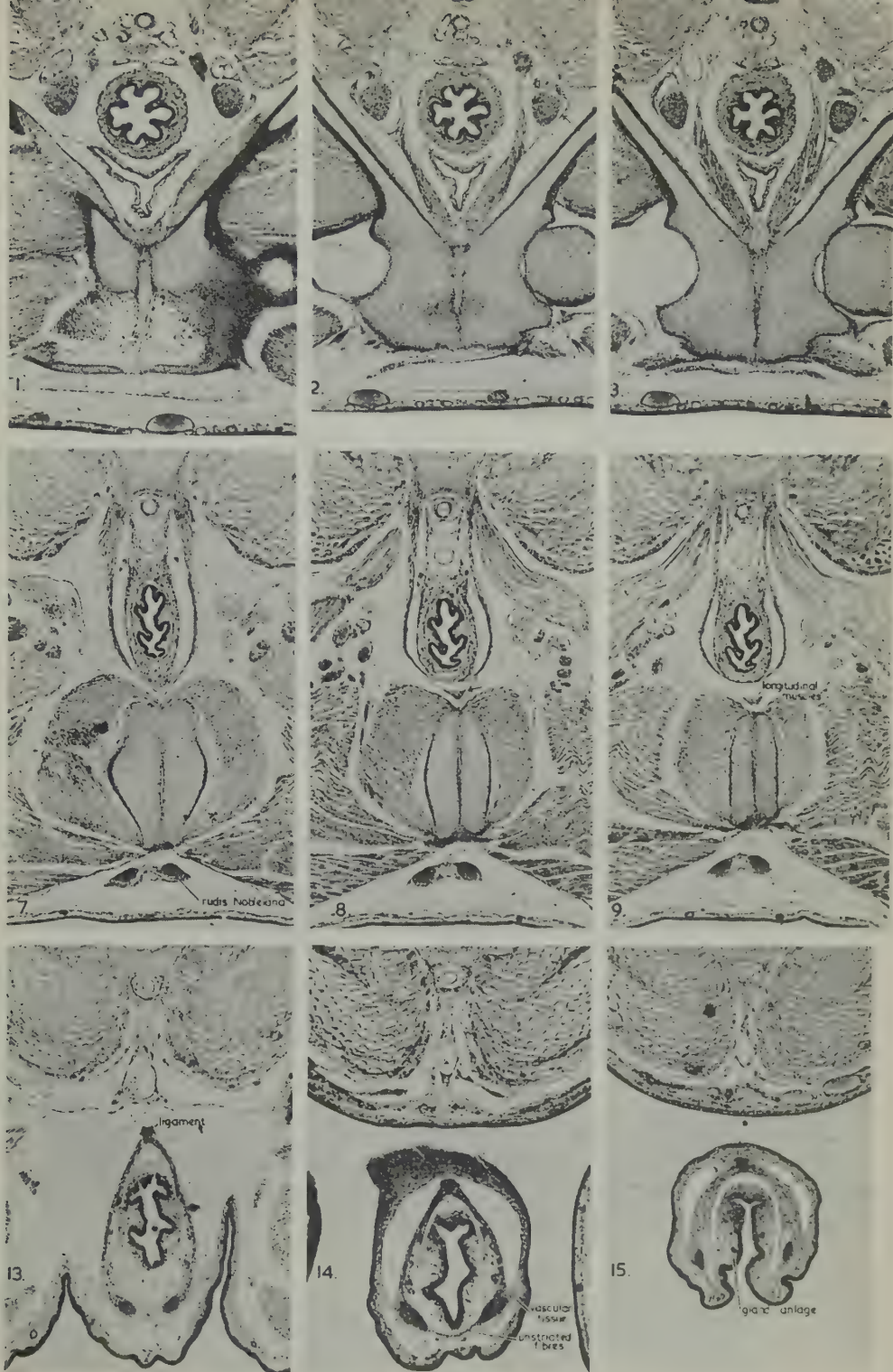


Fig. 21.
 Norma posterioris. Photomicrographs of transverse sections.
 (The number refer to levels in fig. 20.)
 The arrows in the figure at levels 2 and 3 indicate the m. circumflexor arteriae,



at level 8 the arrow indicates the ventral longitudinal muscle cord, and the arrows at levels 16 and 17 indicate a myocomma between myomeres of the m. abdominis rectus.

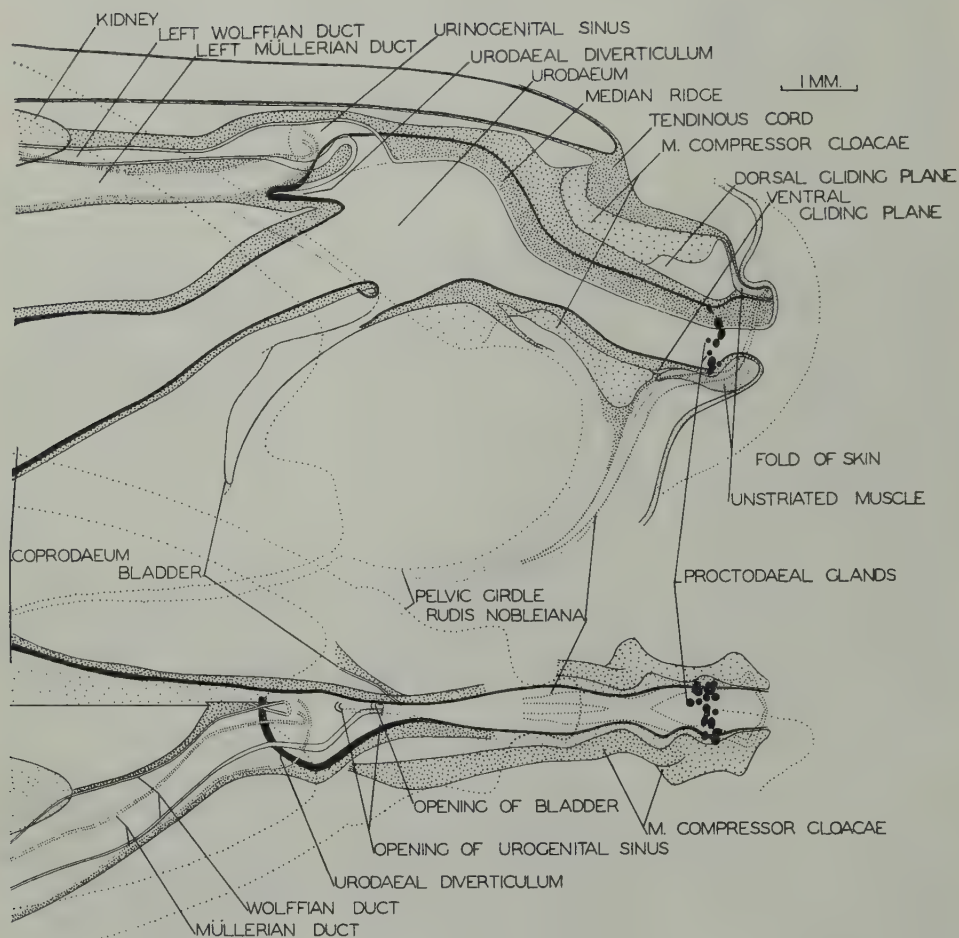


Fig. 22.

Ascapthus adult female. Pelvic region $\times 10$.

Graphic reconstruction from transverse sections (simplified after van Dijk, 1955).
Norma lateralis sinistra (above) and Norma dorsalis (below).

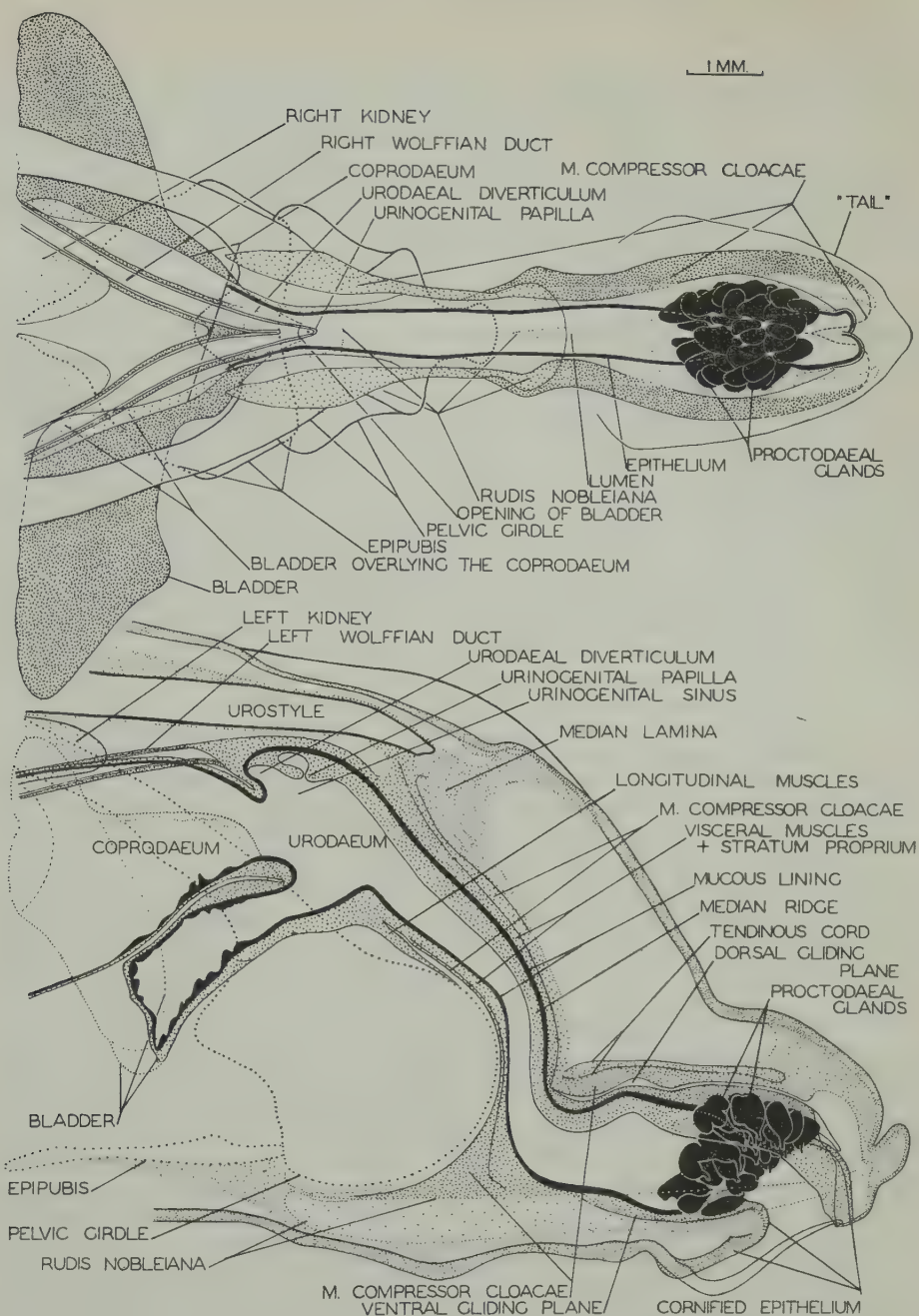


Fig. 23.

Ascapus adult male. Pelvic region x 10.

Graphic reconstruction from transverse sections (simplified after van Dijk, 1955).
Norma lateralis sinistra (below) and Norma dorsalis (above).

THE DEVELOPMENT OF THE PROCTODAEUM AND ASSOCIATED STRUCTURES IN *ASCAPHUS*

In the following descriptions reference will be made to illustrations of the stages described above, but not to the illustrations of the adult conditions (figs. 22, of the female, and 23, of the male).

Structures of Ectodermal Origin

Proctodaeal Invagination: The relation of the proctodaeal invagination to the blastopore could not be determined from the limited *Ascaphus* material available.

Proctodaeal Aperture: The proctodaeal aperture in Stage 47 is situated on a prominence ventral and anterior to the tail fin, from which it is isolated by a notch (fig. 2). At Stage \pm 50 the skin anterior to the proctodaeal aperture has expanded laterally and posterolaterally to form a ventral flap covering the hind-limb buds (figs. 3 and 4:2). The proctodaeal aperture is consequently present at the posterior tip of this ventral flap. The notch between the tail fin and the proctodaeal aperture is deeper at this stage, so that the aperture is posterior instead of ventral. At Stage 51 the proctodaeal aperture is directed posterodorsally from the tip of the ventral flap (fig. 5) and is triangular in shape with the base ventrally (cf. figs. 6:8 and 6:9, transverse sections through the ventral flap and the proctodaeum). There is little change up to Stage 56, figs. 8, 9, 10:17 and 10:18 illustrating the condition at Stage 56 well. At Stage 58 the ventral flap has become smaller and the proctodaeal aperture is situated on a prominence which is dorsal to, and which projects further posterior than, the ventral flap (figs. 11 and 12:13—12:18). As this prominence corresponds to the "tail" or "cloacal extension" of the adult the proctodaeal aperture undergoes little further change.

Proctodaeal-Urodaeal Junction: The proctodaeal-urodaeal junction is not distinguishable during development, consequently the anterior extent of the proctodaeum must be considered as being at some level posterior to that part of the hind-gut distinguishable as urodaeum.

Structures of Endodermal Origin

Urodaeum and Coprodaeum: The coprodaeum passes over into the urodaeum posteriorly, the latter being distinguishable as that part of the cloaca into which the excretory ducts, and later the bladder, open. The urodaeum posteriorly abuts on the ectodermal proctodaeum.

Aperture of the Nephric Ducts: At Stage 47 the urodaeum extends into the somatopleura surrounding the proctodaeum as is shown by the nephric ducts opening into a part of the gut which laterally abuts on the body wall (fig. 1, right side). At Stage 51 there is a single common nephric aperture at the tip of a well-marked ridge in the dorsal wall of the urodaeum, in a region within the coelom. The aperture of the nephric duct moves slightly caudad during subsequent development, changing from a level just behind the posteroventral edge of the 9th spinal myomere at Stage 51 to half-way across the 10th spinal myomere at Stages 56 and 58, reaching to just posterior

to the ventrolateral edge of the 10th spinal myomere at Stages 62—63 and 63. The nephric ducts shift dorsally during development as a consequence of a similar movement of the gut in this region.

Urodaeal Diverticulum: At Stage 62—63 a slight anterodorsal diverticulum has developed anterior to the excretory aperture, and this develops slowly in subsequent stages (figs. 16, 18, 20; compare figs. 21 : 3 and 21 : 4).

Bladder: The anlage of the bladder is present in Stage 51 as a thickening of the ventral wall of the urodaeum, joining the latter to the floor of the coelomic cavity (figs. 5 and 6:1—6:3). It does not involve endoderm (gut epithelium) at this stage. At Stage 56 (figs. 8, 9, and 10:3—10:6) the bladder has developed a lumen, this presumably being a diverticulum of the urodaeum (and hence presumably lined with endoderm) projecting into the previously solid mesodermal anlage. Anteriorly the bladder is free from the gut dorsal to it, and from the floor of the coelom ventral to it, and is externally and internally bifid with anterodorsally directed horns (figs. 9 and 10:3—10:5). Further posteriorly the bladder is attached to the floor and side-walls of the coelom by membranes (figs. 10:3—10:6). The bladder retains its connexions with the coelomic walls while it increases in size in subsequent stages. At Stages 58 the lumen of the bladder begins to show convoluted outlines anteriorly (fig. 12 : 2), by stage 64 the anterior region of the bladder shows many epithelial folds.

Structures of Mesodermal Origin

Coelomic Cavity: At Stage 47 the coelom does not extend dorsally as far posterior as the level of the aperture of the nephric ducts (fig. 1), while laterally it extends posteriorly a short distance beyond the anterior margins of the hind-limb buds (fig. 2). At Stage \pm 50 the relations of the coelom to the tissue of the hind-limb buds is similar. The coelom may be seen to extend posteriorly to a level not far from the posteroventral edge of the 9th spinal myomere (fig. 3). At Stage 51 the coelom reaches to the level of the bases of the hind-limb buds and extends considerably posterior to the level of the aperture of the nephric ducts, reaching to the posteroventral edge of the 10th spinal myomere (figs. 5 and 6 : 5). The coelom extends further posteriorly at Stage 56, reaching a level well within the region of the bases of the hind limbs and slightly beyond the posteroventral margin of the 10th spinal myomere (figs. 8, 9, 10 : 9 and 10 : 10). At Stage 58 the posterior edge of the coelom is still approximately level with the posteroventral margin of this myomere, at Stages 62—63 and 63 it has moved posteriorly half-way towards the posteroventral margin of the 11th spinal myomere and has come to correspond in extent with the posterior limit of the pelvic girdle. At Stage 51 the coelom does not extend far into the tissue between the series of spinal myomeres of the two sides; at Stage 56 it extends approximately $\frac{2}{5}$ of the way from the ventral limits of these myomeres to the vertebral column (cf. figs. 5 and 8, and 6:1—6:5 and 10:1—10:10). In later stages the coelom extends somewhat further upwards. Lateral to the spinal myomeres the posterior limit of the coelom lies close to, and nearly parallel with, the lateral margins of the myocomma between the 8th and 9th spinal myomeres, anterior to them at Stage \pm 50, posterior to them at Stage 56 (cf. figs. 3 and 8).

Splanchnic and Somatic Mesoderm: Splanchnic and somatic mesoderm are continuous with each other at the posterior limit of the coelom and a sharp distinction cannot be made between them. Nevertheless examination of sections close to the posterior limit of the coelom (fig. 15) does reveal that their individuality might be represented in the muscle layers arising in association with them. Somatic striated muscles laterally are distinguishable from splanchnic unstriated muscles medially to them; whether this distinction is valid in the post-coelomic tissue, which contains both these types of muscles, is uncertain.

Visceral Muscle Layers:

Circular Muscle Layer: Posterior to the bladder in Stage 51 the circular muscle layer of the gut is complete for a short distance; further posterior it is incomplete ventrally although present dorsally almost as far caudad as the point at which the limb buds project from the abdomen (figs. 5, 6:5 and 6:6). Ventrally, laterally and dorsally the circular muscles extend into the tissue behind the coelom. At Stage 56, and subsequent stages, the relations are little changed (figs. 10:6—10:13); the circular muscle layer is still complete behind the coelom although the latter extends further posterior than in earlier stages; the dorsal part of the circular muscle layer still extends to approximately the same level.

Longitudinal Muscle Layer: The longitudinal muscle layer of the gut is not as distinct as the circular layer at any level of any stage. This is partly due to the circular muscle layer being more easily distinguished by virtue of its arrangement being more easily detected in transverse sections; but the longitudinal layer does seem to be less developed, particularly posteriorly. The longitudinal muscle layer, in the early stages, is distinguished also from the coelomic epithelium only with difficulty, while posterior to the coelom it is often so close to the mm. compressores cloacae as to be difficult to detect. At Stage 56 the longitudinal muscle layer cannot be detected with certainty posterior to the coelom. At Stage 58 the longitudinal muscle layer is detectable dorsolateral to the gut (see figs. 12:11 and 12:12) almost to the level of the posterior tip of the ventral flap. At Stages 60 and 62—63 the fibres are detectable dorsolateral to the gut as far posterior as just anterior to the cloacal aperture (figs. 13 and 14:3, cf. 14:4; 16 and 17:2, cf. 17:3). At Stages 63 and 64, particularly the former, there are suggestions of the longitudinal layer extending further ventrally at the corresponding levels. The situation is complicated in these stages by increasing development of a gliding plane dorsal to the cloaca and apparently between the circular and longitudinal muscle layers. At Stage 58 there are paired concentrations of longitudinal muscle fibres between the gut and the pelvic girdle near the posterior edge of the latter (figs. 12:8 and 12:9). At the same level longitudinal muscle fibres turn posterodorsally dorsolateral to the gut and approach the vertebral column. These concentrations of longitudinal muscle fibres dorsal and ventral to the gut become better developed in subsequent stages until in Stage 64 it is seen that a substantial proportion of the longitudinal fibres attach to the urostyle above and the pelvic girdle below (cf. figs. 22 and 23). At Stage 64 the longitudinal muscle layer ventral

to the gut forms paired concentrations as in earlier stages, but these combine posteriorly to form a single dense cord triangular in cross-section (apex downwards) before attaching to the pelvic girdle (figs. 21 : 6 and 21 : 9). There are only slight indications of the paired origin of this cord except at the point of attachment to the girdle. The cords of longitudinal muscle fibres passing posterodorsally to the urostyle appear to give way further posteriorly to fibres passing anterodorsally from the post-pelvic gut (cf. figs. 17 : 1 and 17 : 2; 21 : 7—21 : 9).

Anlagen of Pelvic Limbs and Girdle:

Pelvic Limbs: The anlagen of the hind limbs develop ventral to the spinal myomeres on either side of the gut, and anteriorly overlap the coelom slightly (fig. 2, Stage 47). The anlagen bear similar relations to the gut and the coelom at Stage \pm 50. At this stage the anlagen may be seen to be closely associated with the ventral limits of the 9th and 10th spinal myomeres, being just beneath the 10th and a caudad projection of the 9th myomere. Lateral to these spinal myomeres a dorsolateral projection of each anlage, representing the region of the ilial wing, may be seen on either side. Hind-limb buds are present as posterior projections of the hind-limb anlagen from the posteroventral aspect of the abdomen. The hind-limb buds are covered ventrally by the ventral skin flap (figs. 3 and 4 : 2). At Stage 51 the limb anlagen are no longer associated with the 9th spinal myomeres, as the caudad projections of the latter have disappeared. The dorsal limits of the bases of the hind-limb buds are at the level of the ventral margins of the myocommata between 10th and 11th spinal myomeres (fig. 5). At Stage 56 the base of the hind limb of each side reaches the ventral aspect of the 11th spinal myomere posterodorsally (fig. 8). The *m. pyriformis* and the *m. caudalipuboischiotibialis* project into the limb posterior to the ventral margin of the myocomma between the 10th and 11th spinal myomeres.

Pelvic Girdle: The pelvic girdle develops from paired chondrifications in a sheet of dense connective tissue which extends between and over the ventral surfaces of the spinal myomeres, just anterior to the point at which the gut passes posteroventrally through this sheet (figs. 3, 4 : 1 and 4 : 2). Extensions of this sheet laterally constitute the anlagen of the ilia and their muscles (Stage \pm 50, figs. 3 and 4 : 2; Stage 51, figs. 5 and 6 : 4). Paired chondrifications develop in this connective tissue and approach each other at Stage 56, the gut being lifted above the region of their approximation (figs. 8, 9 and 10 : 3—10 : 7). By Stage 58 the halves of the pelvic girdle are separated posteriorly only by a narrow layer of dense connective tissue, while anteriorly they are still well separated (figs. 12 : 8 and 12 : 3). By Stage 60 the halves of the pelvis have fused posteriorly. The anlagen of the iliac regions of the pelvic girdle are directed towards the anterior tips of the lateral margins of the myocommata between the 10th and 11th spinal myomeres. This is seen at Stage \pm 50 (fig. 3) and Stage 51 (fig. 5). When the pelvic anlagen have chondrified (Stage 56) the cartilaginous ilia lie nearly horizontally (in the transverse plane) with the ends turning dorsally (figs. 8, 9, 10 : 6 and 10 : 7). Dense connective tissue continues from the tip of each ilium towards the posterior bay in the lateral face of the

10th spinal myomere. At Stage 58 this bay is approached by the cartilaginous ilium, while the dense connective tissue at the tip of the ilium extends into the myocomma between the 10th and 11th spinal myomeres in a notch in this bay (fig. 11). The ilium is somewhat closer to the notch, which has deepened, at Stage 60 (fig. 13); while at Stage 62—63 the ilium enters the further enlarged notch (fig. 16). The ilia take in progressively more nearly ventro-dorsal positions (in the transverse plane) by addition laterally of dorsally directed portions, and by reduction in width and ventral extent of the spinal myomeres separating the ventral parts of the ilia (cf. figs. 10 : 7, 12 : 5, 21 : 2 and 21 : 3). From a condition where the ilia and the ventral parts of the pelvic girdle lie in the same transverse plane (Stage 56, figs. 8 and 9) there is progressive change in the relative anterior-posterior positions of the ilia and the ventral parts of the girdle. The ilia rotate anteriorly as they penetrate between the 10th and 11th spinal myomeres while the anterior limit of the ventral parts of the girdle remains more or less constant with reference to the spinal myomeres, the posterior limit, however, steadily extends backward from Stage 62—63 to Stage 64 (figs. 16, 18 and 20).

Epipubis: Paired chondrifications develop in the connective tissue anterior to the halves of the pelvic girdle, and are fused to the latter at Stage 58 (figs. 11 and 12:1—12:4). These cartilages are halves of the epipubis and have fused together anteriorly by Stage 60 (fig. 14 : 2). Incomplete fusion of the halves of the epipubis posteriorly results in the presence of a posterior notch in the epipubis of the adult (cf. Stage 64, figs. 21 : 16 and 21 : 17 with 21 : 1). The state of the epipubis anlagen at earlier stages (Stage 56) is best considered with the epipubic muscles.

Rods of Noble and Interfemoral Ligament: At Stage \pm 50 strands of dense connective tissue extend from the ventromedial edges of the hind-limb buds along the sides of the gut close to the ventral flap (fig. 4 : 2). At Stage 51 the same situation is observed, the dense connective tissue disappearing posteriorly into less dense tissue lateral to the gut which extends dorsally to the posterior limits of the bases of the hind-limb buds (fig. 6 : 7). At Stage 56 the strands have developed into the rods of Noble, extending posteriorly from the ventromedial edges of the halves of the pelvic girdle to curve somewhat dorsally on either side of the gut behind the pelvic girdle (figs. 8, 9 and 10:6—10:16). A pair of posterodorsally directed cords of connective tissue above the gut ends close to the tips of the rods of Noble. These cords constitute the beginnings of a dorsal interfemoral ligament. The posterior tips of the rods of Noble and the dorsal interfemoral cords are enclosed in thickenings on either side of the gut. Posterior to this the gut is thin-walled (figs. 10:13—10:16). At Stage 58 this thin-walled part of the gut has disappeared and the rods of Noble and the dorsal interfemoral cords end in the rounded cloacal lips (figs. 11 and 12:15—12:18). The rods of Noble show little change in relation to neighbouring structures in subsequent stages. The anterior tips of the rods at Stage 60 end in a layer of connective tissue which stretches to the ventral surface of the epipubis. This tissue becomes progressively more distinct and at Stage 64 forms a well-marked tendinous sheet (cf. figs. 11, 13, 16, 18, 20 and 21:2—21:6). The dorsal interfemoral ligament at Stage 58 has attained a condition which remains up

to Stage 63. At Stage 64 the ligament slopes somewhat anterodorsally from the cloaca, whereas in Stages 58, 60, 62—63 and 63 the direction is more nearly vertical with the dorsal end turned posterodorsally (figs. 11 and 12:15—12:18; 13; 16 and 17:4—17:6; 18 and 19:2—19:4; 20 and 21:11—21:15). The ligament is a median structure ventrally, but is paired dorsally with the arms passing on either side of the caudal vein.

Somatic Muscles:

Abdominal Muscle Cords (Rectus Muscles): At Stage 47 the abdominal musculature is represented by two cords which separate from the ventral surfaces of the myomeres of the tail (fig. 1) and pass anteroventrally and somewhat laterally. These muscle cords pass over the anterodorsal edges of the hind-limb anlagen (fig. 2), between these and the coelom. Reduction of yolk in the abdominal region results in a more cephalad and less ventrad direction of the abdominal muscle cords, as at Stage \pm 50. The abdominal muscle cord of each side is clearly segmented at Stage \pm 50 and the posterior-most segment is applied to the 9th spinal myomere (fig. 3). A small separate element is present on the inner face of the last abdominal myomere (9th, as it corresponds to the 9th spinal myomere) near its posterior end (figs. 3 and 4:1). There is a small gap between the posterior tip of the last (9th) abdominal myomere and the anterior tip of the hind-limb anlage (fig. 3). At Stage 51 the abdominal cords do not reach dorsally to the 9th spinal myomeres, but curve around the ventral surfaces of the 10th spinal myomeres and pass up the medial faces of these myomeres and the myomeres behind them. (The posterior limits of the cords could not be distinguished.) The 10th and 11th spinal myomeres are ventrally indented by the abdominal cords (figs. 5 and 6). Segmentation of the abdominal muscle cords is clearly shown at Stage 52, the relation of the abdominal myomeres to corresponding spinal myomeres also being possible (cf. description of Stage 52). The 1st abdominal myomere is absent, the 2nd rudimentary; the 9th meets the spinal myomeres. The n. iliohypogastricus, derived from the 8th spinal nerve and used for identifying myomeres, passes into the myocomma between the 8th and 9th abdominal myomeres. This situation is also found in Stage 56 (fig. 8), the 8th abdominal myomeres forming two broad ventral sheets separated by connective tissue (linea alba) while the 9th abdominal myomeres reach up to the ventral surfaces of the 10th spinal myomeres and curve medially round them. Slight ventral notching of the 10th spinal myomere is visible. (See figs. 9 and 10:1—10:6). Just anterior to the ventromedial edge of the myocomma between the 10th and 11th spinal myomeres of each side, the 10th abdominal myomere begins and stretches over the medial faces of the 10th, 11th and 12th spinal myomeres, just reaching to the 13th (figs. 8, 9 and 10, particularly 10:16). The 10th abdominal myomere is apparently the last, but the possibility must be borne in mind that this late-developing segment may derive material from more than one metamere without a myocomma developing between the fibres derived from each. At Stage 58 the 9th and 10th (?+) abdominal myomeres of each side have degenerated, the latter to such an extent that muscle fibres are no longer distinguishable. The remnants of these myomeres are associated with the medial aspect of the

ventrolateral edge of the 10th spinal myomere in much the same position as that occupied by the 9th abdominal myomere at Stage 56 (figs. 11 and 12:1—12:5). At Stage 60 the dorsal part of the degenerated myomeres is absent and the remnants still present do not reach as far as to the spinal myomeres (fig. 13). In subsequent stages these abdominal myomeres are absent. At Stage 58 each 8th abdominal myomere attaches to the epipubic cartilage of that side (figs. 11 and 12 : 1); at subsequent stages these myomeres approach each other more closely anterior to the epipubis, but show little other change in their relations to the latter (figs. 14 : 1 and 14 : 2; 21 : 16 and 21 : 17). At Stage 58 a superficial layer of secondary muscle develops on the ventral surface of the abdominal myomeres. The fibres are distinguishable by their more basophilic staining properties, characteristic of undifferentiated muscle, and by the oblique direction of the fibres in transverse sections (fig. 12 : 1). There is increasing development of this superficial layer in subsequent stages (figs. 14 : 1 and 14 : 2; 21 : 16 and 21 : 17).

Obliquus and Transversus Muscles: At Stage 58, while the 9th and 10th abdominal myomeres degenerate, differentiation of the obliquus and transversus muscles begins between the remaining abdominal myomeres ventrally and the spinal myomeres dorsally (fig. 12 : 1). There are no apparent indications of the origin of the obliquus and transversus muscles from either the remaining abdominal or the spinal myomeres.

Epipubic Muscles and Anlagen of the Epipubis: At Stage 56 the mm. epipubici may be identified as two widely-separated myogenic masses which anteriorly are in contact with the ventromedial edges of the 9th abdominal myomeres, extending along these as far as the myocommata between these myomeres and the 8th abdominal myomeres. Ventral to these developing muscles are the more diffuse anlagen of the epipubis, and beneath these, sheets of connective tissue (figs. 8, 9 and 10:1—10:4). The anlagen of the epipubis are posteriorly separate from the halves of the pelvic girdle, being connected to them by thin vertical strands of connective tissue (fig. 10 : 4); the mm. epipubici posteriorly reach to the pelvic girdle. The anlagen of the epipubis are derivatives of the connective tissue between and beneath the 9th abdominal myomeres, the two anlagen being separate from one another as well as from the pelvic girdle (as mentioned above). The connective tissue in which these anlagen arise might possibly be considered as linea alba although the fibres continue laterally around the abdominal myomeres and are not confined between them. The relations of mm. epipubici show that they should be regarded as secondary derivatives of the abdominal myomeres, either the 8th or 9th or both.

Femorococcygeal and Crurococcygeal Muscles: The tissue from which these muscles (mm. pyrifformes and mm. caudalipuboischiotibiales respectively) arise is that at the posterior limit of the hind-limb bases (fig. 6 : 6). This tissue is associated with the medial faces of the abdominal muscle cords, where these lie on the anterior tips of the medioventral faces of the 11th spinal myomeres (Stage 51, fig. 5). At Stage 56, when the muscles are well differentiated, the same relations are preserved. It is seen at this stage that the part of the abdominal muscle cord with which the muscles of each side are associated is the 10th (?+) abdominal myomere, nearer its posterior end (figs. 8, 9 and 10:9—10:12). At Stage 58 the degeneration of the

abdominal muscle cords has resulted in the association of the mm. pyriformes and mm. caudalipuboischiotibiales with the medioventral faces of the 11th spinal myomeres. The lengthening of the mm. pyriformes and mm. caudalipuboischiotibiales results in their association with the medial faces of the 11th, 12th and 13th spinal myomeres at Stage 62—63, the latter of these muscles just reaching to the 14th spinal myomeres (figs. 16 and 17:3—17:6). At Stages 63 and 64 the mm. pyriformes extend to, and a short distance over, the medial faces of the 14th spinal myomeres (figs. 18 and 19:1—19:3; 20 and 21:8—21:13), while the mm. caudalipuboischiotibiales just reach to these myomeres.

Femoropelvic and Cruropelvic Muscles: These muscles develop from the myogenic material around the pelvic girdle and femur. At Stage 56 the mm. pectinei originate entirely on the halves of the pelvic girdle. At Stage 58 an additional origin is developing on each side, a slip of each m. pectineus passing mediad over the m. epipubicus in the direction of the medial edge of the epipubic cartilage of that side (fig. 12:1). At Stage 64 the epipubic origins are well developed (fig. 21:17).

Coccygeopelvic Muscles: The mm. coccygeiliaci, which constitute in the adult the only muscles present between the pelvic girdle and vertebral column in the cloacal region (except the cloacal muscles), are not distinguishable at Stage 64. They are clearly derived from the spinal myomeres posterior to the ilia, the first of these being the 11th spinal myomeres. Comparison of their attachments to the urostyle in the adult with the origins of the mm. pyriformes suggests that the 11th, 12th and 13th spinal myomeres may contribute to the mm. coccygeiliaci (cf. Stage 64, fig. 20).

Cloacal Compressor Muscles: At Stage 56 the mm. compressores cloacae may be distinguished in the lateral walls of the coelomic cavity, and extend from near the posterior tip of the halves of the pelvis to the end of the coelom and beyond to a level just posterior to the bases of the hind limbs. Ventrally the muscles are attached anteriorly to the posterodorsal tips of the halves of the pelvis, and posteriorly to the rods of Noble; dorsally the muscles extend over the medial faces of the 10th (?+) abdominal myomeres, separated by these myomeres from the medial faces of the 11th, 12th and 13th spinal myomeres. The mm. pyriformes and mm. caudalipuboischiotibiales are interposed between the mm. compressores cloacae and the abdominal myomeres just behind the coelom (figs. 8 and 10:8—10:12). At Stage 58 the mm. compressores cloacae have extended anteroventrally on either side of the opening of the bladder, and posteriorly to the tips of the rods of Noble and the dorsal interfemoral ligament (figs. 11 and 12:5—12:18). The mm. compressores cloacae extend further dorsally and the anterior edges come to acquire, in subsequent stages, (figs. 13, 16, 18, 20 and 21:2—21:15), a more vertical position by anterodorsal expansion.

Arterial Circumflexor Muscles: At Stage 56 slips of muscle continuous with the mm. compressores cloacae near the latter's anterior edges extend anterolaterally, a dorsal slip extending along the ventral half of the medial face of the 10th abdominal myomere of each side, and a ventral slip curling around the arteria ischiadica and the nervus ischiadicus at the point at which the artery twists caudolaterad over the nerve (figs 8 and 10:8). At Stage 58 the dorsal slips of muscle cannot be distinguished. The ventral slip of muscle, or m.

circumflexor arteriae, of each side is more distinct at Stage 58 and subsequent stages (figs. 11 and 12 : 7; 13; 16; 18; 20 and 21:1—21:3). At Stage 60 the point of attachment of each m. circumflexor arteriae to the corresponding m. compressor cloacae is close to the ventral attachment of the latter to the pelvic girdle (fig. 13), and this allows the m. circumflexor arteriae to shift antero-laterally relative to the anterior edge of the m. compressor cloacae during subsequent development. At Stage 64 there are indications of the continuation of the lateral-most edge of the m. circumflexor arteriae medioventrally, so that a complete loop is formed around the artery and nerve (figs. 21 : 2 and 21 : 3). The arteria ischiadica is clearly occluded by the m. circumflexor arteriae in the sections of all stages in which it appears. Whether this was true of the living specimens, and if so to what degree, is impossible to state (cf. figs. 21 : 1 and 21 : 4 with figs. 21 : 2 and 21 : 3).

Unstriated fibres of the mm. compressores cloacae: At Stage 62—63 a cord of tissue is present between the rods of Noble just anterior to the cloacal orifice (fig. 17 : 3). This cord is separated from fibres of the circular and longitudinal muscle layers. In Stage 63 (figs. 19:1—19:4) the cord is visible in the same position, clearly separate from the circular and longitudinal muscle layers anteriorly (fig. 19 : 1), less clearly further posteriorly. At Stage 64 the cord is well separated from these layers (fig. 21 : 14 and also 21 : 15). This cord occupies the position of unstriated muscle fibres occurring in the adult, particularly the female.

Cavernous Tissue: The cavernous tissue characteristic of the cloaca of the adults, female as well as male, has not developed by Stage 64, but there are indications of rudiments. At Stages 62—63, 63 and 64 there are distinct deeply-staining regions lateral to the rods of Noble, anterior to, and anterolateral to, the cloacal orifice (figs. 17 : 3 and 17 : 4; 19:1—19:4; 21 : 14 and 21 : 15).

Lymph Spaces: At Stage 51 there are no lymph spaces associated with the pelvic region. At Stage 56 lymph spaces have developed under the skin of the legs and extend ventrally beneath the pelvic girdle to a point anterior to the ilia (fig. 10 : 5). Medially the lymph spaces extend both caudad and cephalad from the bases of the hind limbs above the level of the rods of Noble. Lymph spaces have begun to separate the rods of Noble from the ventral skin, but are absent in the ventral flap of skin (figs. 10:7—10:10). At Stage 58 lymph spaces extend ventrally as far anterior as the epipubis (fig. 12 : 2), posteriorly small lymph spaces have begun to develop ventral to the rods of Noble posterior to the pelvic girdle (figs. 12 : 9 and 12 : 10). At this stage lymph spaces are also extending into the cloacal "extension" dorsolaterally (figs. 12:15—12:17). At Stage 62—63 there are lymph spaces ventral to the post-pelvic gut and these extend posteriorly as small ventrolateral spaces in the cloacal "extension". The lymph spaces dorsolaterally situated in the cloacal "extension" are well developed at this stage (figs. 17:1—17:6). The lymph spaces present at Stage 62—63 are enlarged at Stages 63 and 64 with little change in relations.

Gliding Planes: At Stage 58 a gliding plane develops dorsally between the gut epithelium and the mm. compressores cloacae near the cloacal aperture (figs. 12 : 16 and 12 : 17). At Stage 60 ventral gliding planes develop ventrolaterally between the gut epithelium and the mm. compressores cloacae (figs. 14 : 3 and 14 : 4). Both dorsal and ventral gliding planes develop closer to the

mm. compressores cloacae than to the gut epithelium. At Stage 62—63 the dorsal gliding plane has enlarged until it reaches the ventral skin posterolateral to the cloacal orifice (figs. 17:4—17:6). The ventral gliding planes remain much less distinct than the dorsal one, but the former do extend sufficiently far towards each other to be considered as a single ventral gliding plane. At Stage 63 (figs. 19:1—19:4) a strip of tissue lateral (distal) to the dorsal gliding plane has developed and extends around the gut ventrally (fig. 19:3), while the circular muscle layer may be detected dorsally between the gliding plane and the gut epithelium. This suggests that the lateral slip of tissue represents the longitudinal muscle layer. Stage 64 shows little further change in the gliding planes.

Epithelial Structures

Cloacal Glands: At Stage 62—63 thickenings have developed in the epithelium just within the cloacal orifice. These are the beginnings of cloacal glands (figs. 17:4 and 17:5). At Stage 63 the gland primordia are distinguishable from the general cloacal epithelium (figs. 18, 19:3 and 19:4). At Stage 64 they are considerably more developed and are raised from the cloacal epithelium, to which they are attached by narrower stalks (figs. 20 and 21:15). Lumina have not yet developed.

Horny Spines: There is no evidence of the horny spines, which occur on the proctodaeal epithelium of the adult male, at Stage 62—63 (the oldest male larva reconstructed).

THE PROCTODAEUM AND ASSOCIATED STRUCTURES IN ADULT ANURA

In the following attempt at relating adult conditions in *Ascaphus* and other genera to larval conditions in *Ascaphus*, reference will also be made to larval conditions in *Xenopus laevis*, *Bufo angusticeps* and *Bombina pachypus*.

Structures of Ectodermal Origin

Proctodaeal Invagination: Whether the proctodaeum of the adult is, or is not, a persistent blastopore could not be established from the limited *Ascaphus* material available; in *Bufo angusticeps*, however, it was possible to show that the blastopore had closed before the proctodaeum was formed.

Proctodaeal Aperture and Proctodaeal-Urodaeal Junction: In *Bufo angusticeps* there is a reduction of the proctodaeum, during development, similar to that observed in *Ascaphus* between Stages 56 and 58, the portion disappearing in *Bufo* being that traversing the ventral fin. Since the dorsal interfemoral ligament and the rods of Noble of *Ascaphus* surround the cloaca close to its orifice, and a homologous ligament (see below) bears the same relations to the cloacal orifice in *Bufo* and also *Rana*, the proctodaeal apertures of *Ascaphus*, *Bufo* and *Rana* may be considered homologous (cf. figs. 20, 22 and 23). Equivalent losses of the proctodaeum would thus appear to have occurred in these genera during development. The proximity of the interfemoral ligament to the cloacal orifice makes it probable that the proctodaeum extends anteriorly beyond the ligament in *Ascaphus*, *Bufo* and *Rana*, and that the extra length of

Figs. 24—27.
Ascapus adult males (each fig. from a different specimen).



Fig. 24.
 Photomicrograph of a transverse section through the cloaca $\times 25$ with enlargements ($\times 125$) of the junction of transitional and stratified squamous epithelia and of a rudis Nobleiana.

Fig. 27.
 Photomicrograph of a longitudinal section of a rudis Nobleiana $\times 125$, taken from a longitudinal section of the cloaca.

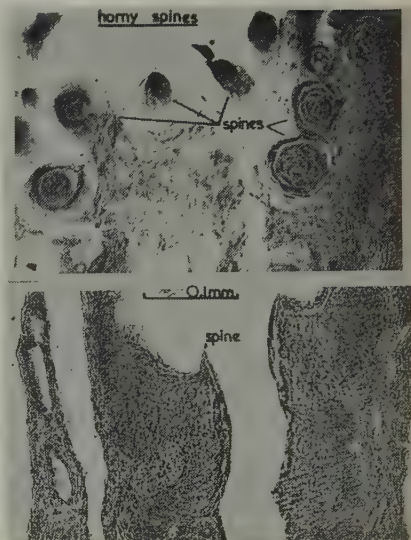
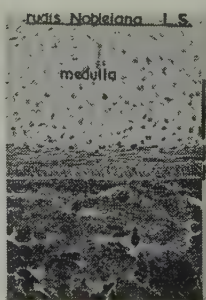


Fig. 25.
 Photomicrographs of transverse and longitudinal sections of horny cloacal spines $\times 125$, taken from longitudinal (tangential) and transverse sections of the cloacal wall.



Fig. 26.
 Photomicrograph of a cloacal gland $\times 125$, taken from a transverse section of the cloaca.

Figs. 28—30.

Ascapbus adult female. Cloaca (norma posterioris).

Photomicrographs of transverse sections. (figs. 29 and 30 are enlargements from fig. 28).

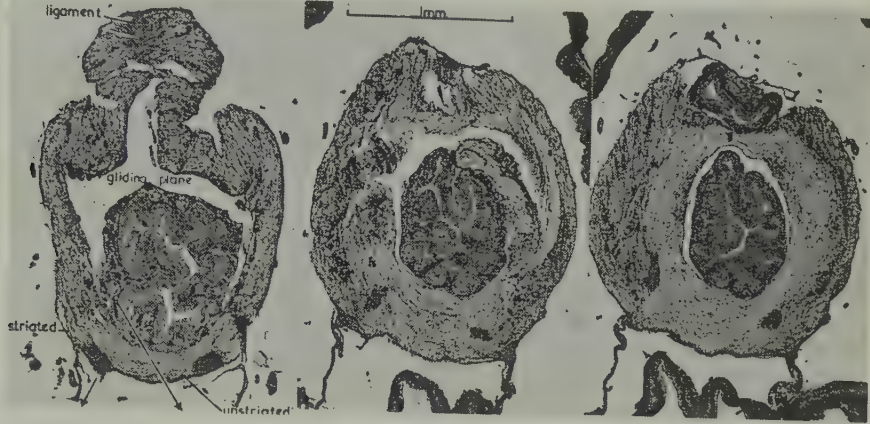


Fig. 28.
Cloaca x 25.

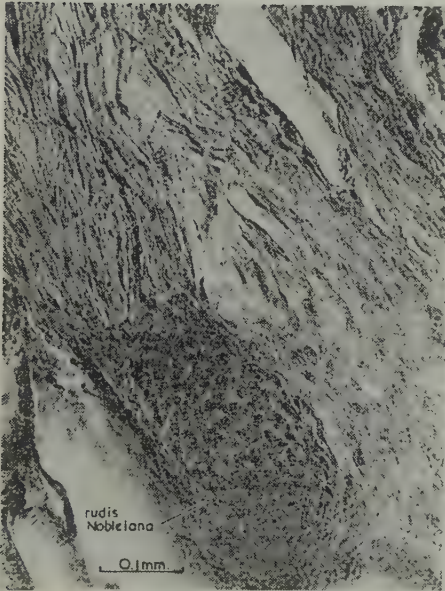


Fig. 19.
Rudis Nobleiana and associated
muscles x 250.

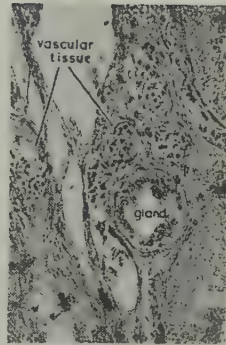


Fig. 30.
Cloacal gland and
vascular tissue.

Figs. 31 and 32.

Rana and *Ascaphus* adult females. Oviducts in the pelvic region.



Fig. 31.
Rana oviduct sectioned
tangentially showing
oviducal glands x 25.

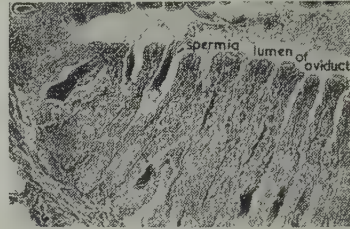


Fig. 32.
Ascaphus oviduct sectioned
transversely showing spermia
x 125.

gut in *Ascaphus* may therefore be either the posterior part of the urodaeum, or the anterior part of the proctodaeum, or both.

Proctodaeal Glands: Dermal glands opening into the cloaca are present in both male and female adult *Ascaphus*, somewhat proximal to the rods of Noble and the dorsal interfemoral ligament (figs. 22, 23, 24, 28 and 30). The ducts of these glands open into a part of the cloaca lined with stratified squamous epithelium. Just anterior to the openings of the ducts the epithelium changes to a transitional epithelium with mucus cells, the line of contact between the two types of epithelium having, like the series of glands, a dorsocaudad slope. (Fig. 24, a transverse section through this region, shows the transitional epithelium dorsally, the stratified squamous ventrally.) this epithelial change may represent a functional change only, or may also represent the proctodaeal-urodaecal junction. If the epithelial change does represent the proctodaeal-urodaecal junction then *Ascaphus* has a relatively longer urodaeum, rather than proctodaeum, than other genera. In any event, it is probable that the cloacal glands are derived from the proctodaeum, rather than the urodaeum, and may hence be referred to as proctodaeal glands. Similar glands, distinct from the neighbouring skin glands, are present in *Leiopelma* near the cloacal orifice.

Horny Spines: Posterior to the proctodaeal glands in the adult male *Ascaphus* the stratified squamous epithelium is raised into horny spines (fig. 25). Such horny structures are characteristic of epithelia of ectodermal origin.

Structures of Endodermal Origin

The junction of the urodaeum with the proctodaeum has been dealt with above.

Structures of Mesodermal Origin

Coelomic Cavity: The posterior extent of the coelomic cavity is much the same in *Ascaphus* as in other genera, the post-pelvic gut ("cloacal extension") of the former being extra-coelomic. The relations of the coelom to the gut are essen-

tially similar in *Ascaphus*, *Leiopelma*, *Xenopus* and *Rana* as may be seen in fig. 40 (except the section of *Xenopus*, which is too far posterior) and fig. 35 : 3 (*Xenopus*).

Visceral Muscle Layers: The circular and longitudinal muscle layers extend along the post-pelvic gut of *Ascaphus*, fibres of the circular muscle layer being distinguishable as far posterior as just anterior to the proctodaeal glands. The extent of the visceral muscle layers thus tends to confirm the localisation of the proctodaeal-urodaeal junction at the stratified squamous and transitional epithelial boundary. The longitudinal muscle layer posteriorly concentrates into dorsal and ventral pairs of cords (taeniae) which attach to the urostyle and pelvic girdle, respectively, in all the genera examined except *Xenopus*, in which dorsal cords are absent. (The relative shortness of the urostyle in *Xenopus* may account for the absence of the dorsal cords.) Some longitudinal fibres continue posteriorly, independent of the cords, except in *Xenopus* and *Leiopelma*. In all the genera examined (except *Xenopus*) the dorsal pairs of longitudinal muscle cords are essentially similar, whereas the ventral pairs show some differences. *Leiopelma* has cords rounded in cross-section; *Bufo* and *Bombina* have well-separated dorso-ventrally elongated cords. (Metamorphosing larvae of the latter two were examined.) The cords in *Rana* are similar to those of *Bufo* and *Bombina*, although somewhat less separated, while in *Xenopus* the cords are more elongated and scarcely distinguishable at two separate entities. In *Ascaphus* the ventral cords are fused into a single cord triangular in cross-section, although the attachments are clearly paired at Stage 64. Tendinous material may be associated with the longitudinal cords near their attachments, in *Xenopus* a sheet of such material lying on either side of the muscle cords while in *Rana* the muscle cords are separated by a fused pair of tendons (cf. ligamentum interfemorale below). (The tendons were taken to be part of the muscle cords in *Rana* in the earlier study, with the result that the erroneous conclusion, that the muscle cords were united, was reached. op. cit., p. 29.) Fig. 40 shows the longitudinal muscle cords in *Ascaphus*, *Leiopelma*, *Xenopus* and *Rana*.

Pelvic Skeletal Structures: The linea alba and interfemoral ligament are conveniently discussed with the pelvic girdle and the epipubis, and are therefore included in this section.

Linea alba: The 8th abdominal myomeres in *Ascaphus* are the last segments of the abdominal cord to occupy positions ventrolateral to the coelomic cavity, the 9th and 10th myomeres (?+), developing lateral to the coelom (fig. 8). The 8th abdominal myomeres approximate medially during later development, those behind them atrophy. It follows that the term linea alba should be applied only to the median ventral fascia as far as the posterior tips of the 8th abdominal myomeres. Further posteriorly the median ventral fascia between the subsequent pairs of myomeres is represented by the ventral, ventrolateral, and even the dorsolateral, walls of the coelom (cf. figs. 8 and 10). It is in, and just ventrolateral to, this part of the median ventral fascia that the epipubis, the halves of the pelvic girdle, and the interfemoral ligament (including the rods of Noble), develop (figs. 8 and 10).

Epipubis: The epipubis and the ilia extend into lateral continuations of the median ventral fascia. In *Leiopelma* the epipubis in the adult underlies the m. rectus abdominis entirely. In *Ascaphus* the m. rectus abdominis attaches more

to the lateral aspects of the epipubis than the dorsal, and is not markedly underlain by the cartilage. This is apparently even more so in *Xenopus*.

Pelvic Girdle: The depth of the symphysis between the two halves of the pelvic girdle results in a dorsal displacement of the cloaca above it. As the tail atrophies during metamorphosis, the cloaca, which had opened at the base of the fully-formed tail, becomes shorter (very little so in *Ascaphus*, particularly the male). The posterodorsal position of the cloacal aperture in adult *Anura* is thus brought about by the shape of the pelvic girdle, the atrophy of the tail, and by the reduction in relative length of the proctodaeum (and possibly of the posterior part of the urodaeum).

Interfemoral Ligament: The septum interfemorale in *Rana* extends medially along the ventral, posteroventral, and posterior edge of the pelvis, from the anteroventral region of the pelvis to the cloaca. Along the length of this septum a strong band of connective tissue, the thickened lateral edges of which contain collagen fibres, extends in *Rana*, *Bufo*, *Bombina*, *Xenopus* and *Leiopelma*. This band of connective tissue has been termed ligamentum interfemorale in view of its relation to the septum termed septum interfemorale in *Rana*. The rods of Noble (and the dorsal ligament — see below), together with the tendinous sheet stretching between these rods and the epipubis are the homologues in *Ascaphus* of the ligamentum interfemorale of the other genera. In *Bufo* the (ventral) interfemoral ligament dorsally extends along the posteroventral edge of the cloacal sphincter muscle, then divides into cords on either side of the cloaca and its muscles. In *Bombina* the ligament forks dorsally as in *Bufo* (and *Ascaphus*), and this condition is clearly the primitive one. In *Xenopus* the ligament in the larva (fig. 36) has similar relations to the gut and is similar in form to the ligament in *Bufo* and *Bombina*, except that the dorsal ends are thickened. In the adult *Xenopus* the dorsal ends of the ligament are very much thickened and serve for the attachment of the mm. compressores cloacae to the pelvic girdle (figs. 35 : 3, 40 and 33). The staining techniques employed (cf. Techniques) showed that the dorsal thickenings in the adult *Xenopus* are of a ligamentous nature and do not consist of unstriated muscle as had previously appeared possible from their histology (van Dijk, 1955, p. 52). In *Rana* the ligament turns forward dorsally and forms a fused pair of tendons which attach to the pelvic girdle between the longitudinal muscle cords (fig. 40). At the point at which the ligament becomes a pair of tendons, the mm. graciles minores originate on the sides of the latter. In *Bufo*, *Bombina* and *Xenopus* the mm. graciles minores similarly originate on either side of the ligament, while in *Ascaphus* these muscles take origin from the homologous rods of Noble. The ligament is present in *Leiopelma* (as mentioned above), but the dorsal part and the mm. graciles minores were apparently removed when the specimen was skinned before sectioning. A short dorsal ligament occurs in *Bufo*, *Bombina* and *Xenopus* on the posterodorsal midline of the cloacal sphincter, much as in *Ascaphus*. It is absent in the adults of *Rana* and *Leiopelma*.

Somatic Muscles:

Epipubic Muscles: That the single m. epipubicus of *Xenopus* is formed from a pair of secondary muscles derived from the m. rectus abdominis, as in the case of the paired muscles of *Ascaphus*, is indicated by the conditions shown in fig. 37. A paired abdominal origin was suggested earlier (van Dijk, 1955, p. 11)

in contradiction to Ryke (1953, p. 54-55) who described a pelvic origin (presumably unpaired). That the m. epipubicus develops asymmetrically in *Xenopus* (as previously suggested, loc. cit.) is shown in figs. 34 and 35 : 1, and the relation of the muscle to the v. abdominalis is also shown in these figures and fig. 33. The presence of the vein on one side (right) may be responsible for the asymmetry. It would appear that the epipubis and epipubic muscles (or muscle) of *Ascaphus*, *Leiopelma* and *Xenopus* are perfectly homologous; but whether the m. epipubicus of *Xenopus* represents one or both of the mm. epipubici of *Ascaphus* and *Leiopelma* is not clear. The condition in *Xenopus* is

Figs. 33 and 34.

Xenopus young adult (both figs. from one specimen). Pelvic region x 25.

Graphic reconstructions from transverse sections.

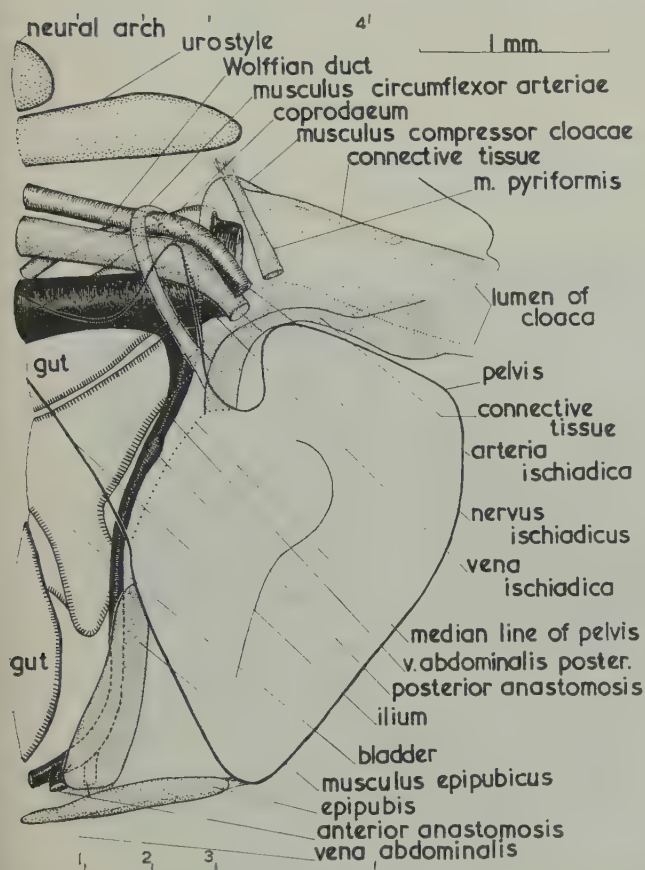


Fig. 33.
Norma lateralis sinistra.

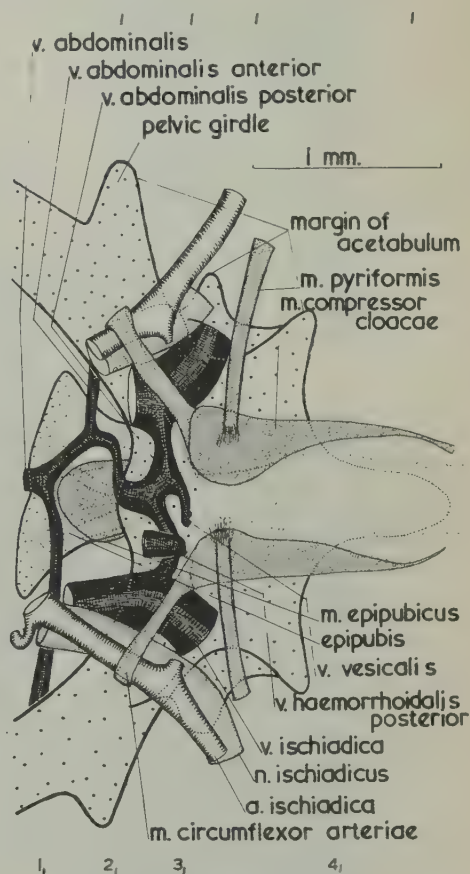


Fig. 34.
Norma dorsalis.

clearly derived by specialization from a condition like that in the *Ascaphidae*. The presence of small cell-aggregations in *Bufo* tadpoles is similar sites to those at which the epipubis anlagen develop in *Ascaphus*, is noteworthy. In *Bombina* tadpoles a substantial cord of connective tissue passes from the linea alba to the pelvic girdle, from which it is isolated ventrally, in a position reminiscent of the m. epipubicus of *Xenopus*. These features of *Bufo* and *Bombina* might indicate that the epipubis was of wide distribution among primitive *Anura*.

Cloacal Compressor Muscles: Distinction may be made between three regions in these muscles, the anterior-most of which is dealt with separately in the next section under the name of Arterial Circumflexors. The other two divisions were termed mm. compressores cloacae and m. sphincter ani cloacalis by Gaupp (1904) (cf. van Dijk, 1955, p. 30). The m. sphincter ani cloacalis comprises that posterior part of the cloacal compressor muscles which is attached neither to urostyle nor pelvic girdle, but forms a complete ring around the cloaca. It is absent in *Leiopelma*, moderately developed in *Rana*, somewhat better in *Bufo* and very well developed by anterior extension in *Xenopus* and by posterior extension in *Ascaphus* (see fig. 33 for *Xenopus*). The whole post-pelvic part of the cloacal compressor muscles in *Ascaphus* actually represents the m.

Figs. 35—37.

Xenopus (each fig. from a different specimen). Photomicrographs of transverse sections $\times 25$. Norma posterioris.

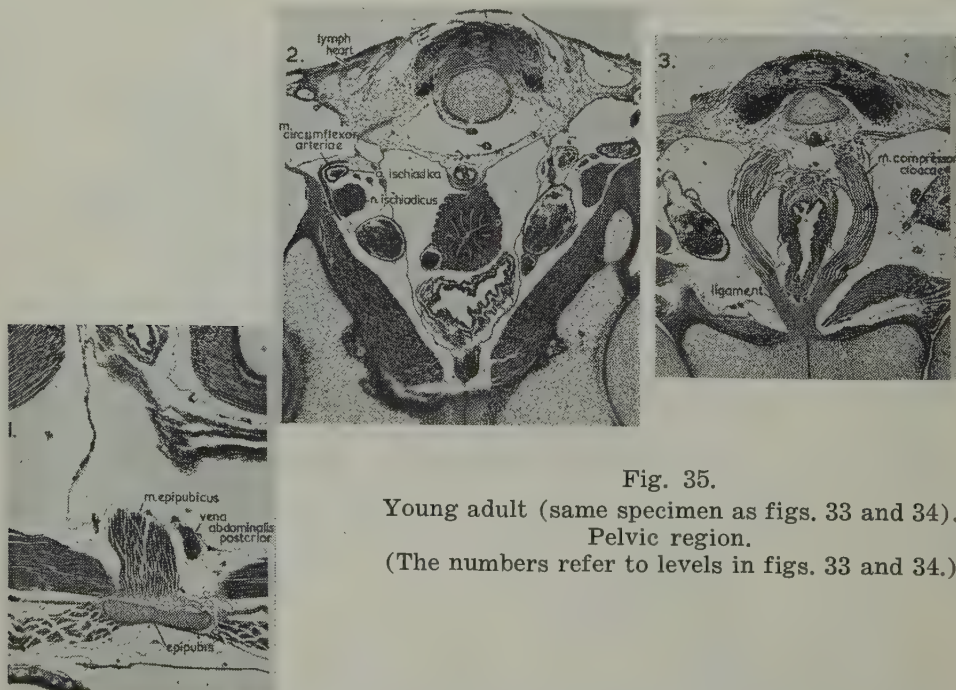


Fig. 35.

Young adult (same specimen as figs. 33 and 34).
Pelvic region.
(The numbers refer to levels in figs. 33 and 34.)

sphincter ani cloacalis (cf. van Dijk, 1955, p. 31). The form of, and the degree of development of, the mm. compressores cloacae, the more anterior division of the cloacal muscles, is similar in *Ascaphus*, *Leiopelma*, *Rana*, *Bufo* and *Bombina*. In *Xenopus* these muscles have the typical form only as far as the tip of the urostyle, this extent constituting a very short length compared to other *Anura*. Behind this region in *Xenopus* the cloacal muscles are attached ventrally to the ligamentum interfemorale, but must be considered as m. sphincter ani cloacalis in view of the complete arch above the cloaca (figs. 33—35 and 40). In *Bufo* and *Bombina* the m. sphincter ani cloacalis attaches to the ligamentum interfemorale at the same level as that at which the mm. graciles minores originate from the posterolateral aspects of the ligament. This is similar to the situation in *Ascaphus* and in contrast to that in *Rana*.

Fig. 36.
Larva. Cloacal region.

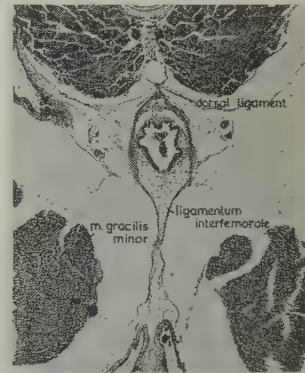
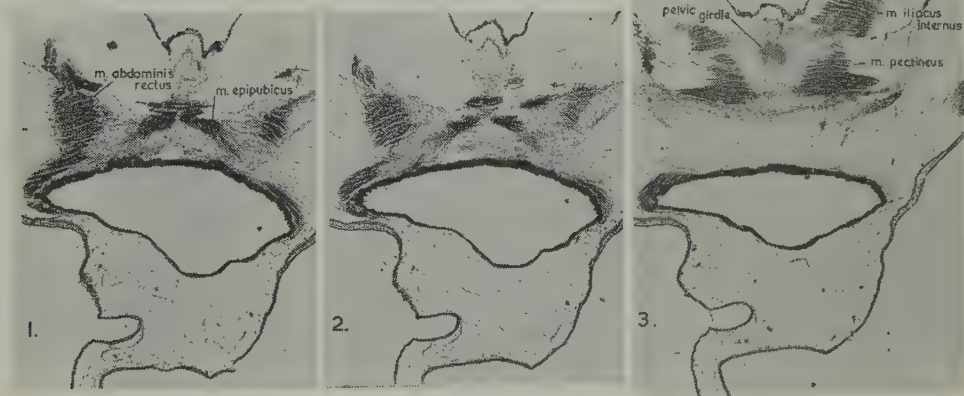


Fig. 37.
Larva. Epipubic region.



Leiopelma adult male (both figs. from one specimen). Iliac region x 25.

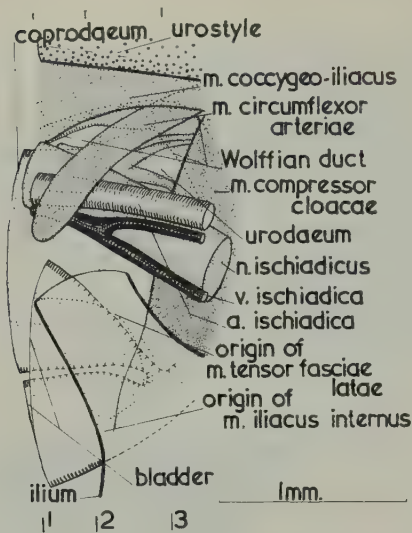


Fig. 38.

Norma lateralis sinistra.
Graphic reconstruction from
transverse sections.

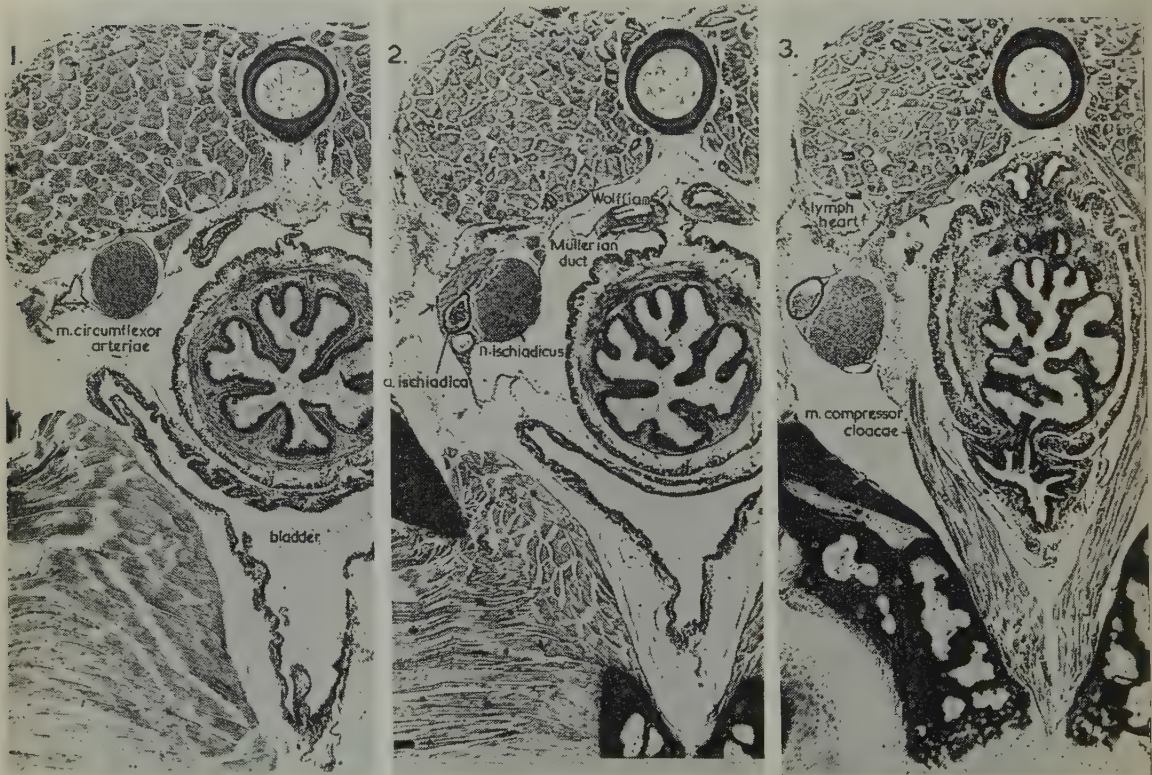


Fig. 39.

Norma posterioris. Photomicrographs of transverse sections.
(The numbers refer to levels in fig. 38.)

Arterial Circumflexor Muscles: At Stage 56 in *Ascaphus* the arterial circumflexor muscles are represented on either side by a slip of muscle detaching from the m. compressor cloacae and dividing into ventral and dorsal portions. By Stage 58 the dorsal portion is no longer distinguishable and the m. circumflexor arteriae is represented only by the ventral portion. At Stage 64 each m. circumflexor arteriae shows a tendency to form a complete loop (cf. figs. 21 : 2 and 21 : 3 with 21 : 1 and 21 : 4). In the adult *Ascaphus*, and some species of *Rana*, complete loops are not formed by these muscles. In *Xenopus*, *Bombina* and *Bufo* complete loops are formed, as was observed in serial sections (figs. 33, 34 and 35 : 3). Dissections of representatives of all the South African anuran families (cf. Materials) revealed that the muscles were present in all cases, and in every case, including *Rana angolensis*, a complete loop appeared to be formed. The muscle is small and the dorsal dissection necessary does not expose it sufficiently to allow the completeness, or otherwise, of the loop to be established with absolute certainty. Sections of *Rana grayi* showed that the very small m. circumflexor arteriae of each side forms an almost complete loop. *Leiopelma* differs from all the other *Anura* examined in that the m. circumflexor arteriae of each side has no connexion with the m. compressor cloacae (figs. 38 and 39) and is clearly derived from the dorsal portion of a slip of muscle extending from the m. compressor cloacae at an earlier stage similar to Stage 56 in *Ascaphus*. In *Leiopelma*, as in all the other *Anura* examined, the m. circumflexor arteriae curves around the arteria ischiadica at the point at which this artery twists laterally over the nervus ischiadicus. It is for this reason, and because the muscle is not associated with the m. compressor cloacae in *Leiopelma*, that the muscle has been termed m. circumflexor arteriae. The occlusion, or partial occlusion, of the a. ischiadica between the n. ischiadicus medioventral to it and the m. circumflexor arteriae dorsolateral to it, seems the only function which contraction of the muscle could perform in *Leiopelma* and the other *Anura*. That the neighbouring coccygeal lymph hearts and their ostia may be influenced, as suggested by Gaupp (1904, p. 364), by contraction of the muscle, is unlikely because of variation in relations of these structures to the muscle. In sections the artery is seen to be partially or completely occluded, but this may be a post-mortem effect. Dissections of preserved and of lightly narcotized (ethyl urethane) specimens showed some constriction of the artery in every case. The relative volumes of blood flowing in the arteriae iliacae of numerous *Xenopus* adults under light narcosis (ethyl urethane), was studied by injection of fluorescein under ultraviolet light, such injections taking place into the dorsal aorta while it was in a position representing as nearly as possible its natural one (cf. Techniques). One m. circumflexor arteriae was cut after an initial injection, and a second injection then given, in every specimen. Changes in the blood-flow were frequently traced to slight movements of the legs occurring during the second injection, and attempts at staking the animal more firmly tended to stop the circulation to the legs. Consistent results could therefore not be obtained. The technique, however, holds promise.

Unstriated fibres of the mm. compressores cloacae: Unstriated fibres are present between the rods of Noble in the female (and, to a much lesser extent, the male) *Ascaphus*, and these fibres have the staining reactions of unstriated muscle. Since these fibres are closely associated with the mm. compressores cloacae (figs. 28, 29 and 21 : 14) it would seem that they are derived from these muscles. The mm. compressores cloacae, widening, have given rise to

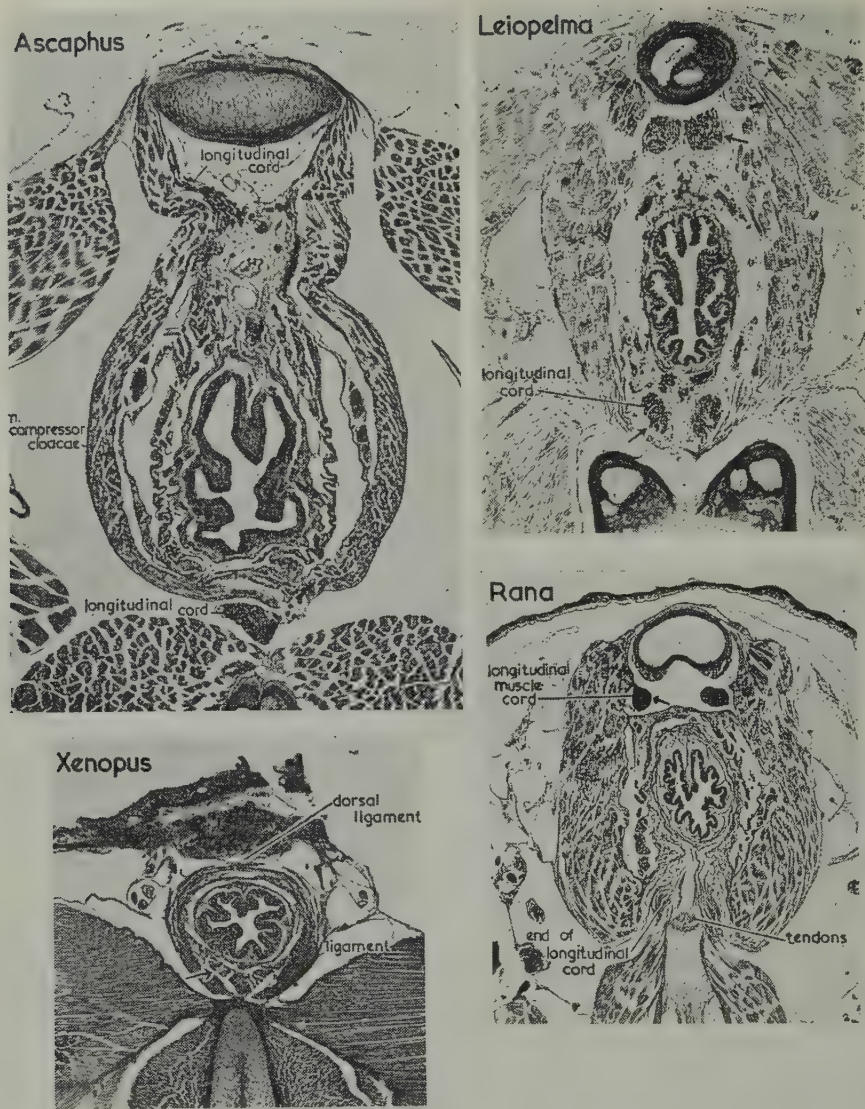


Fig. 40.

Ascaphus, *Leiopelma*, *Xenopus* and *Rana* adults. Cloacas showing longitudinal muscle cords x 25. Photomicrographs of transverse sections. Norma posterioris. The arrows indicate the longitudinal muscle cords. The *Xenopus* section is taken at level 4 of figs. 33 and 34.

Figs. 41—44.

Bufo angusticeps embryos and larvae (each fig. from a different specimen).

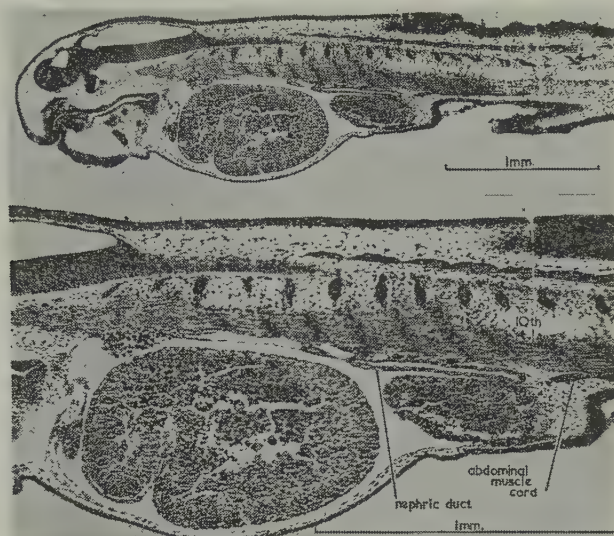


Fig. 41.

Embryo, Stage 42, Trunk region x 25 and x 50.

Photomicrographs of a sagittal section

Norma lateralis sinistra.



Fig. 42.

Embryo, Stage 42.

Cloacal region x 50.

Photomicrographs of

transverse sections

Norma posterioris.

The arrow indicates

the abdominal muscle
cord.

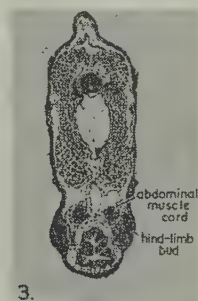


Fig. 43.

Embryo, Stage 46.

Cloacal region x 50.

Photomicrograph of a

transverse section

Norma posterioris.

striated fibres lateral to the rods as well, thus surrounding the rods with striated and unstriated muscle fibres (fig. 28). That the rods are derivatives of the same tissue as the muscles (as previously suggested — van Dijk, 1955, p. 30) is very doubtful.

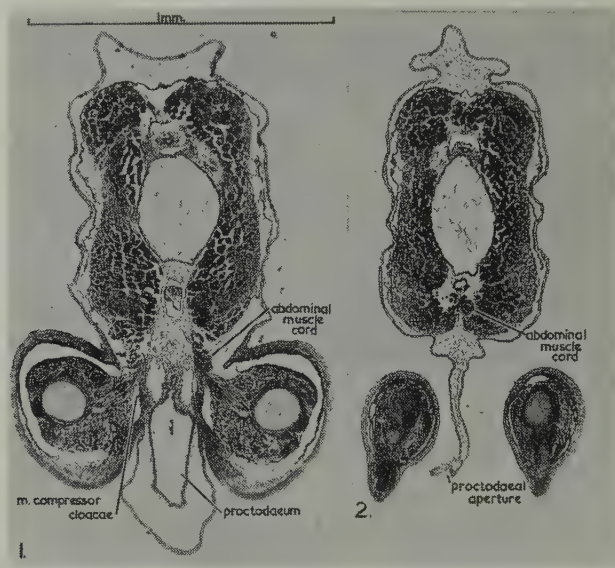


Fig. 44.

Larva, Stage 54.

Proctodaeal region x 50.

Photomicrographs of transverse sections
Norma posterioris.

Cavernous Tissue: The cavernous tissue of the cloaca of *Ascaphus* arises in association with the mm. compressores cloacae and in tissue containing fibres of the circular and longitudinal muscle layers. There does not appear to be de-differentiation of muscle tissue and subsequent vascularization, but rather the vascularization appears to take place in potentially myogenic tissue or in tissue which merely derives a rich vascularization from its proximity to muscle. The median vascularized cord appears to project further posterior in the adult than the point reached by the circular muscle layer at Stage 64. The ventrolateral vascularized cords develop close to the mm. compressores cloacae (figs. 19 : 3 and 19 : 4; 21 : 14 and 21 : 15).

DISCUSSION

A proctodaeal invagination is not the only possible source of an ectodermal, or apparently ectodermal, constituent of the cloaca. "Thus while the micromere layer gives rise to the ectoderm, it apparently also gives rise

to a part of the lining of the archenteron, as LWOFF (Bull. de la Soc. imper. des Naturalistes de Moscou, T. 8, 1894) maintained some years ago" (Wilson, 1901, p. 128). Rugh (1943) gives a description of the neurenteric canal of *Rana pipiens* and observes that "The cells of the floor of the neurocoel, of the floor of the neurenteric canal, and of the roof of the archenteron are of the same type and are, in all probability, continuous in early development" (p. 307). Earlier Erlanger (1891) had come to the conclusion "dass der After aus dem ventralsten Theile des Urmundes hervorgeht, während der dorsalste den Neuroporus und den Canalis neurentericus bildet" (p. 251). Whether the proctodaeum originates as an invagination of ectoderm, or whether it originates as a persistent blastopore (or part thereof) in the *Anura* has been the subject of several studies. Schanz (1887), Morgan (1890) and Erlanger (1891) have given reviews of earlier papers. The formation of the anus from a persistent blastopore (or part thereof) has been reported for numerous animals: by Shipley (1885) for *Petromyzon*; Caldwell (1885) for *Ceratodus*; Sedgwick (1884) and Johnson (1884) for *Triturus cristatus*, Johnson and Sheldon (1886) for *Triturus* sp., Morgan (1890) for *Ambystoma* and Brachet (1902) for *Ambystoma tigrinum* (*Siredon pisciformis*); among the *Anura* by Spencer (1885) for *Rana temporaria*, Kupffer (1887) for *Rana temporaria* (?) and *Alytes obstetricans*, Gasser (1882) for *Alytes obstetricans*, and Pasteels (1942) for *Discoglossus pictus* and *Xenopus laevis*. The formation of the proctodaeum from a proctodaeal pit independent of the blastopore has been reported by Hatschek (1881) for *Amphioxus*, Scott (1880) for the lamprey; among *Anura* by Stricker (1860) for *Bufo cinereus*, Bambeke (1868) for *Pelobates fuscus*, Goette (1875) for *Bombina igneus*, Schultze (1884) for *Rana fusca*, Durham (1886) for *Rana* sp., Sidebotham (1888) for *Rana temporaria*, Morgan (1889 and 1890) for *Rana haeleina* and *Bufo lentiginosus*, Erlanger (1891) for *Rana fusca* and *R. esculenta*, *Bufo variabilis* and *B. vulgaris* and *Bombina igneus*, by Ziegler (1892) for *Rana* sp., Brachet (1902) for *Rana temporaria*, Marchetti (1918) for *Bufo vulgaris*, Rondinini (1928) for *Bufo vulgaris*, Vogt (1929) for *Bombina*, Kagawa (1932) for *Bufo vulgaris japonicus*, Schechtman (1939) for *Hyla regilla* and Pasteels (1942) for *Rana fusca* and *Rana esculenta*, *Bufo vulgaris* and *Hyla arborea*.

Studies of Bytinski-Salz (1936), Risley (1939) and Schechtman (1939) were undertaken to elucidate the mechanism of proctodaeum formation and cloacal plate perforation. Schechtman (op. cit.) working on *Hyla regilla* suggested the following mechanism: "The ventral lip mesoderm induces the proctodaeal pit in that portion of the ectoderm which happens to come into contact with it. The invagination of the pit brings it into contact with the entoderm of the hind-gut. The latter completes the process of anus formation by inducing the perforation of the proctodaeal pit" (p. 49—50).

Risley (1939) remarked of anus formation in urodeles: "It is of particular interest that, under experimental conditions, a secondary anus may appear in conjunction with secondary tails even though no blastopore formation or gastrulation has occurred" (p. 114). This suggests that the formation of the "anus" from a part of the blastopore is not necessarily the primitive condition.

Pasteels summarizes the development of the proctodaeum as follows: "Le blastopore présente chez les Anoures deux modes d'évolution: chez les uns (*Discoglossus*, *Xenopus*), il se transforme en anus sans subir d'occlusion transitoire; chez les autres (*Rana*, *Bufo*, *Hyla*, probablement *Bombinator*), il s'obture de façon précoce, l'anús apparaissant à la suite d'une perforation

secondaire. . . Ces différences ne correspondent qu'à une variante chronologique dé la même cinématique" (1942, p. 25).

In the descriptions of the formation of the proctodaeal pit, the position, in relation to the mesoderm, at which the cloacal membrane is formed, is rarely mentioned. Schanz (1887) does note of the proctodaeal pit that it had been supposed that "ein Stück des Urdarms wüchse ihm entgegen, . . ." (p. 10), and Marchetti (1918) observes that "Le cellule sticotropiche del fondo delle due fossette si vanno incontro, e per potersi raggiungere e fondere scacciano il mesoderma interposto" (p. 237).

The proctodaeum develops as an ectodermal fossa in *Bufo angusticeps*. The region of the cloaca into which the bladder and the nephric ducts open is apparently endodermal in *Ascaphus* (fig. 1) and *Bufo* (figs. 41, 42 and 43), as is inferred from the presence of yolk in the cloacal walls. According to Gadow's (1887) terminology this region may be described, by definition, as urodaeum. The urodaeum of *Ascaphus* and *Bufo*, then, is apparently endodermal. Shumway (1942) uses Gadow's terminology (Americanised) in describing the cloaca of the chick: "No urinary bladder is formed but the cloaca is ultimately divided into three regions: an anterior portion, the coprodeum, into which the rectum enters; an intermediate part, the urodeum, into which the urogenital ducts enter, and the terminal proctodeum" (p. 147). From this description it is clear what should be understood by cloaca and rectum. Unfortunately, other authors have been less precise. Huettner (1949) states of the young larval *Rana*: "The cloaca being continuous with the proctodaeum, is therefore partially formed by ectoderm. Its inner portion, which is continuous with the rectum, is formed from entoderm. Later on the *urinary bladder* is developed from the endodermal region of the cloacal portion of the hind-gut" (p. 134). This description does make it clear that the urodaeum is endodermal, at least ventrally, in Huettner's opinion. The region of the cloaca into which the nephric ducts open, is variously referred to as "cloaca", "rectum" and "proctodeum" in "NORMAL TABLE OF XENOPUS LAEVIS (DAUDIN)" edited by Nieuwkoop and Faber (1956). Thus the Wolffian ducts are said to open into "rectal diverticula" which originate as follows: "The *rectal diverticula* are indicated for the first time at STAGE 32, at which they appear as tiny slits in the dorsal wall of the proctodeum" (p. 132). It is further noted (p. 135, op. cit.) that "The *urinary bladder* develops as a ventral diverticulum of the rectum at STAGE 55 . . .". On p. 157 it is stated: "At its posterior end the rectum is continued beyond the last coil of the ileum, and then becomes the *cloaca*. The cloaca receives the ureters which enter by two separate openings lying close to one another in its dorsal wall. On the ventral side the cloaca communicates with the *urinary bladder*."

A study of O'Connor (1940) on *Pleurodeles waltii*, *Triturus taeniatus* and *Ambystoma* indicated that the posterior part of the gut might attract the nephric ducts during development and that the terminal parts of the ducts in adults might have a cloacal origin. Bijtel (1948), working on in *Triturus alpestris*, found that grafts of presumptive cloacal material attracted the nephric ducts to it during development. She refers to this material as "matériel cloacal", but refers to that which develops from it as a secondary proctodaeum. "Il est patent que le proctodaeum secondaire a exercé dans ce cas, donné en exemple, une action attractive sur l'uretère primaire". Bijtel noted one limitation: "Si regrettable que ce soit, la transplantation d'un peu de matériel sométique est inévitable". It is also important to emphasize that the exact limits of the

proctodaeum, in an animal in which it does not develop as a proctodaeal pit (as appears to be the case in urodeles), are difficult to determine. In *Xenopus* the cloaca is described as developing diverticula which grow anteriorly in the direction of the nephric ducts, later fusing to these (Nieuwkoop and Faber, editors, see above).

There is little literature on the development of the cloacal muscles in chordates. Lineback (1920) investigated the origin and development of the longitudinal muscle layer of the colon of *Homo* and refers to earlier remarks on the development of the visceral muscles in mammals; but in neither his own work, nor, apparently, in the works cited by him, is the relation of these muscles to the coelom described. The later development of the somatic muscles of the gut of *Homo* has been studied by Popowsky (1899), but the origins of these muscles would seem to be obscure. In *Tachyglossus* the sphincter cloacae appears to be a dermal muscle as it is continuous with the dermal muscles of the abdomen (Ruge, 1895). (Ruge's illustration appears in Wiedersheim's *Vergleichende Anatomie der Wirbeltiere* and other textbooks.)

Goette (1875) observed the relation of the abdominal muscle cords to the pelvic region. "Das hinter dem Becken gelegene Stück lässt er teils atrophieren, teils soll aus ihm das M. ischiococcygeus werden," to quote Lignitz (1897), p. 32. The m. ischiococcygeus is, in Gaupp's nomenclature (1896), the m. compressor cloacae. The abdominal muscle cords ("die ältesten Bauchmuskeln" — Kaestner) were subsequently studied by Kaestner (1892, 1893a and 1893b), Wiedersheim (1892), Field (1894) and Wild (1897), while Lignitz (1897) referred to their findings (except those of Wild) critically. Field and Lignitz were interested in the development of the fore-limbs. Maurer (1892), investigating the development of the trunk and abdominal muscles of urodeles, does not appear to have observed similar relations to the pelvic region in the case of the urodelan abdominal muscles as occur in the *Anura*. Green (1931) mentioned that "The 'primary abdominal muscle' preceding M. rectus abdominis at first passes through the pelvic basin to a point posterior to this. During the closure of the pelvis it moves forward and becomes attached to the pubic symphysis (p. 1287, of *Rana*). Recently Ryke (1953) described the development of the somatic muscles of the trunk of *Xenopus*, stating in his introduction (p. 2): "I do not intend reviewing the literature prior to MAURER, as it has been fully dealt with by this author in his above-mentioned works. Suffice it to say, that these include the publications of MECKEL (1828), DUGES (1835), STANNIUS (1854), HUXLEY (1873), GOETTE (1875), SCHNEIDER (1879) and KÄSTNER (1892)." The works of Maurer referred to are those of 1892 and 1895. Goette is later mentioned by Ryke in connexion with the m. sternohyoideus and appears in his bibliography, the other works mentioned (other than Maurer's) are not cited in the bibliography. Wiedersheim (1892), Kaestner (1893a and 1893b), Wild (1897), Lignitz (1897) and Green (1931) are not referred to at all. Ryke observed the abdominal muscle cords in the pelvic region: "An interesting point in the development of the m. rectus abd. is the occurrence (sic) of a backwardly directed strip reaching the root of the tail (fig. II) (sic). It runs along the outer side of the cloaca and possibly represents the m. rectus lateralis of some fishes. During metamorphosis this muscle strip atrophies" (p. 19). The m. rectus lateralis is situated much further dorsally than the abdominal muscle cords, being found at the level of the horizontal myoseptum.

The significance of the abdominal muscle cords for the interpretation of

the development of the pelvic muscles is summarized by Wild (1897, p. 33) as follows: "Kästner selbst sagt, dass es ganz verkehrt sei, den Versuch zu machen, den Wiedersheim und er selbst unternommen hätten aus einem wohl differenzierten Abschnitte der Bauchmuskulatur die Muskulatur der hinteren Extremität abzuleiten. Auf denselben Umstand macht auch Field . . . aufmerksam: 'Der bereits differenzierte Bauchmuskel habe mit der Bildung der Extremitätenmuskulatur nichts zu schaffen.'" Field (1894) and Lignitz (1897) advanced evidence that the fore-limbs are derived from the spinal myomeres and not from the abdominal muscle cords. Kaestner (1893a and 1893b) and Wild (1897) could not advance much evidence for the derivation of the hind-limb anlagen from the spinal myomeres, but were convinced that the hind-limb anlagen were not derived from the abdominal muscle cords. The present study confirms that the hind-limb anlagen are not derived from the abdominal muscle cords and removes one obstacle to the derivation of these anlagen (and hence also the cloacal muscles) from the spinal myomeres: The abdominal muscle cords are not interposed between the hind-limb anlagen and the spinal myomeres at Stage ± 50 of *Ascapthus*. This is quite clear although the specimen is by no means a perfect one. It is difficult to understand the relationship of the abdominal cords at Stage 47 to the same muscles at Stage ± 50 , but subsequent development is easily followed. The hind-limb anlagen develop independently of the abdominal muscles in *Ascapthus*, but differentiation of the cloacal compressor muscles occurs after the abdominal muscle cords have extended backwards to beyond the pelvic region (Stage 51).

When the cloacal compressor muscles first appear in the *Ascapthus* material examined (Stage 56), it is clear that they are not associated with the skin, and are therefore not dermal muscles; but they are quite closely associated with the abdominal muscles and the mm. pyriformes and mm. caudalipuboischiotibiales dorsally, and with the pelvic girdle anteroventrally. It is possible that the cloacal compressor muscles may be late derivatives of the same myogenic tissue which gave rise to the late-developing pelvic parts of the abdominal cords. In *Bufo* the abdominal muscle cords are complete when the hind-limb anlagen are barely indicated (figs. 41 and 42), and the anlagen subsequently develop ventral to the abdominal cords (fig. 43). When the abdominal muscle cords atrophy posteriorly the anterior regions of the mm. compressores cloacae, and, particularly, the mm. circumflexores arteriarum, are closely associated with the atrophying muscles. There is a marked increase in development of the mm. compressores cloacae while the abdominal muscle cords are atrophying in *Ascapthus* (Stages 58—60) and, particularly, in *Bufo* (cf. fig. 44, showing little development of the mm. compressores cloacae and maximally developed abdominal cords). That there may be a causal association between the atrophying of the abdominal cords and the differentiation of the mm. compressores cloacae, is a possibility. Goette (1875) may have been correct in his derivation of the "M. ischiococcygeus" from the abdominal muscle cords. Kaestner (1893a) does not consider the derivation of Goette likely: "Nach meinen Untersuchungen geht jenes hinterste Stück bei Froschlärven ganz zu Grunde. Bombinator igneus scheint sich demnach etwas anders zu verhalten" (p. 280, discussing the abdominal cords). It is worth mentioning that the obliquus and transversus muscles also differentiate, between the abdominal cords and the spinal myomeres, while the abdominal cords are atrophying (Stage 58 of *Ascapthus*), their differentiation not beginning in *Bufo* until atrophy of the abdominal cords is con-

siderably advanced. In the comparison which can thus be made between the differentiation of the cloacal compressors and the obliquus and transversus muscles it is of importance to note that Ryke's (1953) interpretation of the abdominal muscle cords of *Xenopus* as constituting all the abdominal muscle layers anterior to the pelvis (loc. cit., fig. 6, p. 14; fig. 27, p. 39) seems to gain no support whatever from conditions in *Ascaphus* and *Bufo*, and is at variance with Kaestner's interpretation of the obliquus and transversus muscles: "Die erwähnte Muskelschicht liegt überall lateral — bezw. dorsalwärts vom Rectus abdominis, stösst, wenigstens anfangs, nirgends mit ihm zusammen, sondern es findet sich ein muskelfreier Zwischenraum zwischen der lateralen Grenze des Rectus und der medialen der neuen Muskelschicht" (1893a, p. 283).

If the cloacal compressor muscles are neither derived by division of the abdominal muscle cords when these have already formed (which derivation seems most unlikely), nor while these cords are developing or atrophying, another mode of origin from the abdominal muscle cords is still possible. It is possible that, like the mm. epipubici, they are derived in association with, if not from, the myocommata between segments of the abdominal cords. (The possibility that myocommata can contain myogenic elements must be admitted, since the proximity of the epipubic muscles to myocommata in *Ascaphus* suggests a possible histogenetic relationship.) It is probable that the mm. compressores cloacae are pelvic muscles unconnected with the abdominal muscles.

Experimental evidence, such as that obtained by Byrnes (1898), Lewis (1910) and Detwiler (1918 and 1929), has been that "There is no demonstrable contribution of the somites to the musculature of the limb in amphibians". (Nicholas, J. S., in "Analysis of Development" edited by Willier, Weiss and Hamburger, 1955, p. 431.) From the works of Lewis and Detwiler cited, there is evidence that extirpation of somites in the anterior region of urodeles results in the absence of ventrolateral abdominal muscles, but that the fore-limb still develops. Byrnes (op. cit.) found in both *Ambystoma* and *Rana* that suppression of the abdominal muscles is effected by treatment not affecting the hind-limb musculature. It would be interesting to learn to which category the cloacal compressor muscles belong on this criterion. While negative experimental evidence has questionable morphological significance, positive findings would be, at least, suggestive. There is evidence (based on carbon marking technique) that not only the limb buds, but also part of the ventrolateral muscles may form independently of the somites, at least in Aves (Rawles and Straus, 1948; Straus and Rawles, 1953). Detwiler (1955), however, finds the ventrolateral muscles of urodeles to be derived from the somites in studies based on extirpation and xenoplastic grafts. Since the abdominal muscles have already appeared in the earliest *Ascaphus* stage available (Stage 47), the study of their origin was unavoidably beyond the scope of the present investigation.

An investigation of *Salmo* and *Periophthalmus* showed the absence of striated cloacal muscles. Paired longitudinal muscles stretch from the pelvic girdle to the anal-fin skeleton in both of these teleosts, but these are widely separated in the cloacal region in both genera.

The thickening of the septum interfemorale which has here been named ligamentum interfemorale, and which in *Ascaphus* is modified to form the rods of Noble ventrally, was observed by Gaupp (1896) in *Rana*. Describing the m. gracilis minor, he wrote: "Dieser schmale, ganz am medial-hinteren Rande des Oberschenkels gelegene Muskel entspringt mit dem der anderen Seite von einem

sehnigen Streifen, der den hinteren Rand der Beckenscheibe deckt, vorn an der Insertion des *Rectus abdominis*, hinten an der *Spina pelvis posterior* befestigt ist. An dem hinteren Abschnitte dieses Streifens, bis zum Ursprunge des *Gracilis minor*, entspringen die hinteren Bündel des *Sphincter ani*" (p. 182). Grobbelaar (1922) did not mention this "sehniger Streife", but described the m. gracilis minor as originating on the ischium, close to the symphysis, in *Xenopus*. Bigalke (1926) divided the m. gracilis minor (M. cutaneous femoris) into a Caput superius and Caput inferius, referred to Gaupp's description and stated: "Bei *B. vulgaris* aber entspringt das Caput superius, zusammen mit dem der anderen Seite, mit dünnem Ursprung gerade unterhalb der Afteröffnung von der hinteren Fläche des M. sphincter ani cloacalis und nimmt gleich an Breite beträchtlich zu" (p. 335). In both *Xenopus* and *Bufo* the ligament is nevertheless present. In *Xenopus* the ventral and dorsal parts were reconstructed and labelled "connective tissue" before their significance was realized (fig. 33). In *Ascaphus* the rods of Noble bear essentially similar relations to the cloaca and the mm. graciles minores as do the dense edges of the ligamentum interfemorale in other *Anura*. Since the possession of these rods has been regarded as evidence of great specialization in *Ascaphus*, this genus must now be considered as being less specialized than has been maintained. The glands of the oviduct in which spermia are to be found in *Ascaphus* are essentially similar to the oviducal glands of *Rana*, as may be seen from figs. 31 and 32. Here specialization for internal fertilization has not produced any marked morphological changes.

Szarski (1957), discussing the larval state in *Amphibia*, observed: "All amphibian and fish larvae have a similarly constructed tail fin, consisting of a skin fold." The shortening of the proctodaeum during metamorphosis, which occurs in the *Anura*, would thus also take place in fish larvae when the tail fin becomes reduced. This may be seen, for example, in Stages 27 and 28 of the development of *Gasterosteus aculeatus* (Swarup, 1958).

Bufo exhibits no marked specializations in the cloacal region which distinguish it from the other *Anura* studied. Green (1931) remarked that "the oldest definitely accepted Anuran is of Upper Jurassic age (*Eobatrachus agilis* March; Moodie 1912)" and "*Eobatrachus* is structurally almost indistinguishable from modern Bufonids" (p. 1259). In respect of the cloacal region there is no reason to believe that this is not because the bufonids are rather primitive *Anura*. *Rana* and *Xenopus* reveal several specializations in the cloacal region, while *Bombina* resembles *Bufo* quite closely. Szarski's evidence that *Rana* shows greater specialization than *Bufo* and *Bombina* in the vascular system (1948) is significant in the light of conditions in the cloacal region. *Ascaphus* and *Leiopelma* show specializations from the bufonid condition in the cloacal region, and these are typically in divergent directions. An example is afforded by the enlargement and modification of the m. sphincter ani cloacalis in the male *Ascaphus* and the absence of this muscle in *Leiopelma*.

In *Ascaphus* and *Leiopelma* there is one more presacral vertebra than in typical *Anura* such as *Bufo*, and this is regarded as a primitive feature. Green (1931) offers evidence of this and remarks: "The phylogenetic forward extension of the ilia is represented during larval development" (p. 1288). Smit (1953) states: "If we consider that during the evolution of the *Anura* a forward shifting of the ilio-sacral articulation has taken place (Watson, 1939—1940, and Piveteau, 1937), . . . then the urostyle must represent original trunk vertebrae, as suggested by Piveteau (1937), and not caudal vertebrae" (p. 127—128). Despite the dif-

ference in sacral vertebrae in the *Ascaphidae* (in which it is the 10th vertebra) and in *Bufo* and *Rana* (in which it is the 9th) the plexus ischiadicus and the innervations of the pelvic muscles, including the mm. compressores cloacae, is essentially the same. Information in this connexion has been given for *Ascaphus* by Ritland (1955a and b), and van Dijk (1955), for *Leiopelma* by Stephenson (1952) and Ritland (1955b), for *Rana* by Gaupp (1899) and others; and for *Bufo* by Bigalke (1926). Goodrich (1930) remarked of movements of the hind-limb: "For instance, in the frog the straining backwards of the pelvic plexus shows that the base of the hind-limb has moved backwards with the elongation of the pelvic girdle" (p. 138). The innervation of the cloaca by the 11th spinal nerves in *Rana*, by the 11th, 12th, and sometimes the 13th (according to Ritland) spinal nerves in *Ascaphus*, and by 11th to 13th nerves in *Leiopelma* (as appears to be the case), suggests a process of transposition (Rosenberg, 1875 and 1907) by which the innervations have been shifting to more anterior nerves during phylogeny. On the other hand it is clear that the hindlimbs shift backwards relative to the spinal nerves during ontogeny. Comparison of Stages 56 and 64 of *Ascaphus* (figs. 8 and 21) shows the pelvis moving from a position ventral to the 12th spinal nerve to one behind the 13th. This movement is even more strikingly illustrated by comparing Stage 56 with Ritland's (1955a) fig. 11 and Stephenson's (1952) fig. 2, when it may be seen that the origin of the 12th nerve, which marks the original level of the pelvic girdle, is far forward on the urostyle in both *Ascaphus* and *Leiopelma*. The same movement of the pelvis clearly takes place in all *Anura* during development. The cloacal nerves of tetrapods are apparently rarely presacral, and it seems likely that the 11th vertebra is the posteriormost sacral vertebra to have occurred in an anuran with the ascaphid arrangement of the plexus ischiadicus. The relation of the sacral plexus to the sacrum in *Urodela* is well illustrated by Davidoff (1884). The 13th spinal nerve is apparently rarely retained in the adult *Ascaphus*, although Ritland has detected it (pp. 166—167 and fig. 11, 1955a) and reports that it supplies the cloaca. In none of the larvae reconstructed in the present study, nor in the adults reconstructed previously (1955) does the 13th nerve participate in the plexus ischiadicus.

Of the tail muscles of the larval *Anura*, only those in the region of the urostyle are retained in the adult, becoming the mm. cocygeo-iliaci. Since these muscles only become differentiated at metamorphosis, when the cloaca has almost achieved its adult form, their development is of little consequence to cloacal differentiation. The differentiation of the spinal myomeres early in metamorphosis has here been studied in *Ascaphus* and the comparative material (*Bufo*). As the youngest *Ascaphus* embryo studied (Stage 47) has well-differentiated spinal myomeres, the earlier development of the spinal myomeres is not relevant to the present study, which is centred on *Ascaphus*. It may be mentioned, however, that there have been a number of studies on the origin of the tail and the early stages of its subsequent development. Notable among the workers in this field is Bijtel, whose thesis (1929) and some of whose subsequent works (Bijtel 1930, 1931, 1936 and 1958) have been consulted in the present study. Other works consulted are those of Chuang Hsiao-Hui (1947), Nakamura (1942, 1947 and 1952) and Bijtel and Woerdeman (1928), as well as others also mentioned in other connexions (e.g. Marchetti, 1919; Rondinini, 1928).

Of the *Amphibia*, the anurans *Ascaphus* and *Nectophrynoides*, the salamandroid *Urodela*, and all the *Gymnophiona* practice internal fertilization.

The copulatory apparatus of *Gymnophiona* has been investigated by Tonutti (1931, 1933) and others (cf. van Dijk, 1955, pp. 51—52), and comparisons with the copulatory apparatus of *Amniota* have been made by Tonutti (1932 and 1934). The cloacal and caudal regions of *Gymnophiona* are specialized, the absence of the pelvic girdle being a notable specialization. For this reason, and because the development of the copulatory apparatus in *Gymnophiona* has not been worked out, the nature of the muscle layers of the cloaca in these animals is obscure and comparisons with amniote conditions must be considered tentative. Since Tonutti further compares the more specialized *Gymnophiona* with specialized *Amniota*, and compares the cloacas of the males while the female condition is probably more primitive, his conclusions must be considered doubtful. In *Nectophrynoides* and those *Urodela* which copulate, the cloaca is little specialized for copulation. The cloaca of *Ascaphus* similarly appears to have undergone relatively slight modifications for copulation when compared with the conditions in most *Amniota* and in *Gymnophiona*. Conditions in the *Anura* and the *Urodela* therefore suggest that internal fertilization developed in early tetrapods without the evolution of a complicated intromittent organ. The absence of an intromittent organ in *Sphenodon* (Gadow, 1887) suggests that such organs evolved late in tetrapod evolution and independently in divergent directions in the *Squamata*, the *Synapsida* (and hence the mammals), and the *Chelonina* and *Archosauria-Aves* lines.

SUMMARY AND CONCLUSIONS

1. In *Bufo angusticeps*, as in other *Bufo* species, the proctodaeum forms from a proctodaeal pit after closure of the blastopore.
2. In *Bufo* the proctodaeal pit meets the archenteron in the tissue posterior to the coelom, i.e. in the somatopleura (somatic mesoderm).
3. In *Ascaphus* the junction between the proctodaeum and the enteron lies posterior to the coelom within the somatopleura (somatic mesoderm) at an early stage.
4. In early stages of *Bufo* and *Ascaphus* the nephric ducts open into a region of the gut (which is hence, by definition, urodaeum) with yolk-laden walls.
5. In *Bufo* and *Ascaphus* the urodaeum, as shown by the presence of abundant yolk in its walls, is part of the endodermal enteron and is (at least initially) endodermally lined. (The urodaeum is widely accepted as being endodermal in *Amniota*.)
6. In *Bufo* and *Ascaphus* the longitudinal and circular layers of visceral muscle develop in the (splanchnic) mesoderm around the endodermal enteron in the coelomic region, and posterior to the coelom in the somatopleural region.
7. Splanchnic mesoderm may have accompanied the enteron into the post-coelomic somatopleural region when enteron and proctodaeum approached each other, thus giving a layer of splanchnic mesoderm between the enteron and somatopleura (somatic mesoderm).
8. The post-coelomic visceral muscle layers in *Bufo* and *Ascaphus* may, like those of the coelomic region, be derived from splanchnic mesoderm.
9. The visceral muscle layers persist behind the coelom in adult *Ascaphus*, *Leiopelma*, *Bufo*, *Xenopus*, *Bombina* and *Rana*.
10. The posterior limit of the visceral muscles probably corresponds closely to the urodaeal - proctodaeal junction in *Anura*.

11. The posterior limit of the visceral muscles in *Ascaphus* corresponds approximately to the level at which there occurs during metamorphosis differentiation of the cloacal epithelium into transitional, proximally, and stratified squamous, distally.
12. The urodaeal-proctodaeal junction in adult *Ascaphus* may be represented by a transitional — stratified-squamous epithelial junction.
13. A cluster of dermal cloacal glands surrounds the transitional — stratified junction in adult *Ascaphus* of both sexes.
14. The ducts of the dermal cloacal glands of *Ascaphus* are directed somewhat posteriorly and thus open into the stratified squamous epithelium region.
15. The dermal cloacal glands of *Ascaphus* develop during metamorphosis as solid thickenings of the stratified squamous epithelium, separating (except for the future ducts) as solid structures from the epithelium and becoming hollowed out later in metamorphosis.
16. There is no evidence that the cloacal glands are not proctodaeal glands. In the light of the evidence that they are of proctodaeal origin they should be considered as proctodaeal glands.
17. In *Leiopelma* there are, at least in the male, glands similar to the proctodaeal glands of *Ascaphus* near the cloacal orifice and distinct from the glands of the skin near them.
18. In the adult male *Ascaphus* horny spines develop in the stratified squamous epithelium of the cloaca, anlagen of these spines not being visible late in metamorphosis.
19. The development of horny spines, which are characteristically ectodermal structures, is further evidence that the proctodaeal part of the cloaca extends at least as far as such spines occur.
20. The cloaca lengthens posteriorly, during development, in traversing the ventral skin flap in *Ascaphus* (and probably *Leiopelma*, which also possesses this structure) and the ventral fin in *Bufo*, *Xenopus*, *Bombina* and probably most other *Anura*.
21. The cloaca in the region of the ventral fin or ventral skin flap is without a tunica muscularis in all the *Anura* examined, and is presumably proctodaeum only.
22. Early in metamorphosis the loss of the ventral flap or the anterior part of the ventral fin results in a shortening of the proctodaeal part of the cloaca.
23. The cloacal lips are differentiated in the adult position before the shortening of the proctodaeum occurs in *Ascaphus*, *Bufo*, *Xenopus* and *Bombina*. This is very well seen in *Ascaphus*.
24. The cloacal lips bear similar relations to the pelvic structures, particularly the septum interfemorale, in *Ascaphus*, *Bufo*, *Xenopus* and *Bombina* and appear to be in homologous positions in these *Anura*.
25. In *Ascaphus*, when the hind-limb buds become distinct (Stage \pm 50), the pelvic anlagen are situated immediately ventral to the spinal myomeres at the level of the 10th and caudad processes of the 9th of these myomeres.
26. The topography of the 9th, 10th and 11th spinal myomeres (especially the 10th), is such as to make their contribution to the anlagen of the pelvic muscles, or their derivation from the same source as these anlagen, possible and even probable.

27. Anterior to the pelvic anlagen in *Ascaphus* (Stage \pm 50) the 9th myomeres are differentiated into spinal myomeres dorsally and abdominal myomeres ventrally; further cephalad (8th myomeres etc.) there is a separation of spinal and abdominal myomeres.
28. In *Bufo* the 10th trunk myomere is divided into a spinal myomere dorsally and an abdominal ventrally and anterior to this the abdominal myomeres, from their first appearance, are separate from the corresponding spinal myomeres.
29. In *Bufo* and *Ascaphus* the abdominal myomeres thus form abdominal muscle cords metamERICALLY segmented in a manner corresponding to the segmentation of the spinal myomeres with which they are (at least initially) continuous posteriorly.
30. In *Ascaphus* the 9th abdominal myomeres separate from the spinal myomeres early in development (Stage 51) and the 10th, and possibly more caudad, abdominal myomeres develop and project over the faces of the 10th and subsequent spinal myomeres without showing metameric correspondence to them.
31. In *Bufo* the abdominal myomeres extend posteriorly along the ventromedial edges of the 10th and subsequent spinal myomeres, with which they serially correspond.
32. In *Bufo* the hind-limb anlagen are scarcely visible and the hind-limb buds are absent when the abdominal muscle cords are completely formed.
33. In *Ascaphus* the abdominal muscle cords have extended caudad beyond the pelvic anlagen, by development of the 10th myomeres, before the mm. compressores cloacae develop.
34. In *Bufo* and *Ascaphus* the mm. compressores cloacae may be derivatives of the pelvic muscle anlagen or of the abdominal muscle cords.
35. The mm. compressores cloacae differentiate in the region of the somatic mesoderm (somatopleura) lateral and posterolateral to the coelom between the posterior region of the pelvis and a level somewhat caudad to the posterior edge of the coelom. (*Bufo* and *Ascaphus*.)
36. The mm. compressores cloacae are more closely associated (anteroventrally) with the pelvis than with the vertebral column until late in development. (*Bufo* and *Ascaphus*.)
37. The mm. pyriformes in *Bufo*, and these muscles and the mm. caudalipuboischiotibiales in *Ascaphus*, develop near the posterodorsal limit of the mm. compressores cloacae. The posterodorsal limits of the three pairs of muscles in *Ascaphus*, and the two pairs in *Bufo*, lie close together throughout development.
38. There is no evidence of differentiation of the abdominal muscle cords to give rise to the mm. compressores cloacae in *Bufo* or in *Ascaphus*.
39. The mm. compressores cloacae might be late derivatives of the same stratum as had given rise to the posterior parts of the abdominal muscle cords in *Ascaphus*.
40. The abdominal muscle cords in *Bufo* develop so much earlier than the mm. compressores cloacae that late derivation of the latter from the same stratum as gave rise to the former is extremely unlikely.
41. The 9th and subsequent abdominal myomeres atrophy during metamorphosis in *Ascaphus* (Stages 58—60) and *Bufo*.

42. The atrophy of the abdominal myomeres in the pelvic region becomes evident, in *Ascaphus* and *Bufo*, shortly after differentiation of the mm. compressores cloacae takes place.
43. In *Ascaphus* and *Bufo* atrophy of the abdominal muscle cords posteriorly, is closely synchronous with the differentiation of obliquus and transversus muscles in the region between the remaining anterior parts of the abdominal cords (rectus muscles) ventrally and the spinal myomeres dorsally. The beginning of atrophy of the abdominal cords is clearly evident in *Bufo* before the obliquus and transversus muscles develop, and these muscles have differentiated before atrophy of the abdominal cords is complete in *Ascaphus*.
44. There might be causal relation between the atrophy of the abdominal muscle cords and the development of the mm. compressores cloacae and obliquus and transversus abdominal muscles.
45. A superficial secondary muscle layer develops on the ventral surface of the m. abdominis rectus (prepelvic portions of the abdominal cords, separated in the midline by the linea alba), at the time when the abdominal muscle cords are atrophying posteriorly in *Ascaphus*. Such a m. abdominis rectus superficialis has been reported from *Xenopus* (Ryke), but the stage at which it develops is unknown. Ryke could not find the muscle in *Ascaphus*.
46. There is no evidence in *Ascaphus* or *Bufo* that the mm. compressores cloacae develop as secondary derivatives of existing muscles, abdominal or spinal, in a manner comparable with the origin of the m. abdominis rectus superficialis in *Ascaphus*.
47. The mm. epipubici develop as secondary muscles associated with the myocommata between the 8th and 9th abdominal myomeres, in *Ascaphus*.
48. There is evidence that the m. epipubicus of *Xenopus* is a secondary derivative of the rectus muscles as in *Ascaphus*.
49. The mm. epipubici of *Ascaphus* are innervated by the crural (9th spinal) nerves.
50. There is no apparent evidence that the mm. compressores cloacae arise in association with the myocommata of pre-existing segmental muscles, abdominal or spinal.
51. The cloaca of *Ascaphus*, including the mm. compressores cloacae, is innervated by the 11th and 12th spinal nerves, sometimes also by the 13th spinal nerve (Ritland).
52. The mm. compressores cloacae show no indications of dual (or triple) origin. This makes a derivation similar to that of the mm. epipubici unlikely, as the mm. compressores cloacae would originate from cells from more than one myocomma (because of their compound innervation).
53. Early in the development of the mm. compressores cloacae in *Ascaphus* the anterodorsal edges give off slips of muscle curving ventrolaterad and dorsomediad over the faces of the abdominal muscle cords.
54. The dorsomedial slips of muscle from the anterior edges of the mm. compressores cloacae are transient in *Ascaphus*, while the ventrolaterad slips develop around the aa. iliacae and nn. ischiadici, showing a tendency later in development to form loops beginning medially from the mm. compressores cloacae and ending at the pelvis near the midline.
55. In *Leiopelma* there are muscles in the adult occupying the positions of the dorsomedial slips of the mm. compressores cloacae in larval *Ascaphus*, and curving around the aa. iliacae and nn. ischiadici. These muscles are isolated

- from the mm. compressores cloacae and hence have been given a separate name, mm. circumflexores arteriarum. This name is also applied to the homologous muscles in *Ascaphus* etc. (dorsales may be appended to distinguish the *Leiopelma*, ventrales the *Ascaphus*, condition).
56. In all the families of *Anura* found in South Africa mm. circumflexores arteriarum occur and appear to form complete or nearly complete loops extending from the mm. compressores cloacae around the aa. iliacae and nn. ischiadici to the pelvis.
 57. In *Ascaphus* and *Rana* (some species only, apparently, e.g. *R. temporaria* according to Gaupp) the mm. circumflexores arteriarum form half-loops only, the lateral parts being absent.
 58. The mm. circumflexores arteriarum have no known function, but they have the same relation to the aa. iliacae and nn. ischiadici in all the *Anura* examined, whether they are separate from the mm. compressores cloacae as in *Leiopelma* or joined as in other *Anura*.
 59. The aa. iliacae may be compressed against the nn. ischiadici by the mm. circumflexores arteriarum.
 60. The posterior parts of the mm. compressores cloacae meet each other mid-ventrally and mid-dorsally to form a sphincter, the m. sphincter ani cloacalis, in *Rana*, *Bufo*, *Bombina*, *Xenopus*, *Ascaphus* and probably most other *Anura*.
 61. A sphincter ani cloacalis is absent in *Leiopelma*, the cloacal sphincter in this genus consisting of a circular visceral muscle layer.
 62. The teleosts *Salmo* and *Periophthalmus*, have no striated cloacal (anal) sphincters.
 63. The absence of a striated cloacal sphincter in *Leiopelma* may be a primitive feature.
 64. The m. sphincter ani cloacalis is enlarged in the male *Ascaphus* to form the striated muscle layer of the "cloacal extension".
 65. The bilateral origin of the m. sphincter ani cloacalis may be reflected in the presence of fascial sheets in the dorsal and ventral midlines, such fasciae forming thickened cords on the surfaces of the muscles.
 66. The cords on the dorsal and ventral midlines of the m. sphincter ani cloacalis form part of a ligament lying in the septum interfemorale, and hence have together been named ligamentum interfemorale.
 67. Dorsal to the cloaca the ligamentum interfemorale consists of a single dorsal ligament attached to the urostyle, and penetrated by the v. caudalis at least in the larvae, in *Ascaphus*, *Bufo*, *Bombina* and *Xenopus*.
 68. A dorsal ligament is absent above the cloaca in *Rana* and *Leiopelma*.
 69. Ventral to the cloaca the lateral edges of the ligamentum interfemorale are thickened into tendinous cords in *Bufo*, *Bombina*, *Xenopus*, *Rana* and *Leiopelma*, while in *Ascaphus* these thickenings are represented by the rudes Nobleianae (rods of Noble, "post-pelvic" rods, "post-pubic" rods, "Nobelian bones", etc.).
 70. The ligamentum interfemorale stretches from the pubic region along the ventral, posteroventral and posterior edge of the pelvis to the cloaca in *Bufo*, *Bombina* and *Rana*.
 71. In *Xenopus*, *Leiopelma* and *Ascaphus* the ligamentum interfemorale reaches the epipubis anteriorly (= tendinous sheet in *Ascaphus*).

72. In the male *Ascaphus* the rods of Noble are widely separated from the posterior edge of the pelvis and reach to a level just anterior to the cloacal orifice.
73. The ligamentum interfemorale of *Bufo* and *Xenopus*, and the rods of Noble of *Ascaphus* fork posteriorly to extend on either side of the cloaca near its orifice.
74. In *Xenopus* the fork of the ligamentum interfemorale below the cloaca is greatly thickened and extended forwards, and serves to attach the mm. cloacae to the pelvis.
75. In *Rana* the end of the ligamentum interfemorale below the cloaca is turned forward, and it attaches to the pelvis.
76. In *Bufo*, *Bombina*, *Xenopus* and *Rana* the mm. graciles minores originate from the ligamentum interfemorale just below the cloaca. In *Ascaphus* these muscles originate from the rods of Noble in a comparable position.
77. The cloacal orifices of *Bufo*, *Bombina* and *Xenopus* bear the same relations to the ligamentum interfemorale as does that of *Ascaphus* to the rods of Noble: these orifices are hence homologous.
78. In *Leiopelma*, *Bufo*, *Bombina* and also *Rana* (cf. van Dijk, 1955) there are two cords of longitudinal visceral muscle attached to the urostyle, and two to the pelvis, in the cloacal region.
79. In *Xenopus* there are no longitudinal visceral muscle cords attached to the urostyle, and the cords to the pelvis are closely associated with each other.
80. In *Ascaphus* there are two longitudinal visceral muscle cords attached to the urostyle, but there is only one cord attached to the pelvis, although this has a dual origin.
81. The vascularized tissue in the cloacal region of *Ascaphus* develops in association with the visceral muscle layers and the mm. compressores cloacae, but does not arise from de-differentiated muscle tissue.

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